UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DYNAMIQUE ET COEXISTENCE D'ESPÈCES FORESTIÈRES TOLÉRANTES À L'OMBRE: LE CAS DE L'ÉRABLE À SUCRE ET DU HÊTRE À GRANDES FEUILLES

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DOMINIQUE GRAVEL

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AVANT-PROPOS

Cette thèse est constituée de six chapitres rédigés en anglais sous la forme d'articles scientifiques. Au moment du dépôt de la thèse, le troisième chapitre a été publié dans la revue *Ecology Letters*, le cinquième chapitre est en révision dans la revue *Ecology* et les autres chapitres seront soumis sous peu. Je suis le premier auteur de chacun de ces chapitres, mais pour l'ensemble d'entre eux, j'ai travaillé de paire avec d'autres collaborateurs.

Les chapitres I et II ont été réalisés en collaboration avec ma co-directrice Marilou Beaudet et mon directeur Christian Messier. Ensemble nous avons planifié les deux études. J'ai réalisé la collecte des données sur le terrain et au laboratoire, les analyses statistiques et rédigé les manuscrits. Ensemble nous avons discuté les résultats, amélioré les analyses et commenté les manuscrits.

Les chapitres suivants (III à VI) sont le résultat de travaux de modélisation. Pour ces chapitres, les différents co-auteurs ont été impliqués dans la planification des différents modèles de simulation, la discussion des résultats et la correction des manuscrits. J'ai développé la théorie précédant la modélisation, réalisé les simulations (et la programmation des modèles au besoin), l'analyse des données ainsi que rédigé les différents manuscrits.

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RÉSUMÉ

L'intérêt des écologistes forestiers pour la dynamique de l'érable à sucre (*Acer saccharum* Marsh.) et du hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) remonte au fondement de la discipline. Comprendre les déterminants des variations dans la distribution et l'abondance de ces espèces dans l'espace et dans le temps est un objectif qui a été longuement poursuivi et qui est d'intérêt général pour les écologistes forestiers intéressés à la coexistence d'espèces tolérantes à l'ombre. Dans les forêts du sud du Québec, une certaine appréhension de l'augmentation de la présence du hêtre à grandes feuilles dans les érablières a récemment été manifestée. Un tel changement de la composition d'un écosystème forestier dominant dans cette région pourrait avoir des répercussions majeures sur les organismes qui y sont associés ainsi que sur les services que l'on en retire. De façon plus générale, ce problème constitue aussi une occasion intéressante pour mieux comprendre les processus qui affectent la dynamique et l'abondance d'espèces en coexistence.

Deux objectifs généraux ont été proposés dans cette thèse. D'abord, afin d'établir les bases pour la compréhension du récent changement de la dynamique de régénération de l'érable et du hêtre dans les forêts du sud du Québec, le premier objectif vise à décrire la dynamique de ce phénomène et à tester des causes possibles à son origine. En second lieu, par l'étude de ce phénomène et par des études théoriques, nous devrions être en mesure de mieux comprendre les mécanismes qui permettent la coexistence et affectent la dynamique de ces espèces, et plus généralement, d'espèces forestières très tolérantes à l'ombre.

Cette thèse est constituée de six chapitres présentés sous la forme d'articles scientifiques. La thèse est unie par un thème commun : la force de la coexistence en fonction de la similarité des espèces et de l'hétérogénéité environnementale. Les deux premiers chapitres sont empiriques et ils portent spécifiquement sur l'identification des facteurs déterminant les variations spatiales et temporelles de l'abondance relative de l'érable à sucre et du hêtre. Les chapitres suivants sont théoriques, développés à partir de modèles de simulation, et généralisables à une grande variété de communautés d'organismes sessiles. Ces chapitres théoriques sont, entre autres, destinés à compléter la connaissance théorique nécessaire à l'interprétation des résultats observés dans les premiers chapitres.

Il y a effectivement eu une recrudescence de l'abondance du hêtre parmi les gaules à l'échelle du Québec au cours des dernières décennies. L'abondance du hêtre parmi les gaules a presque doublé en dix ans, alors que celle de l'érable est demeurée inchangée. Dans une première étude empirique réalisée à l'échelle de la communauté forestière, le modèle traditionnel de coexistence de ces espèces, basé sur la différentiation des espèces en termes de survie et de croissance au long de gradients de lumière et de fertilité du sol, ne parvient

pas à expliquer la distribution spatiale des gaules à l'échelle locale. La relation entre la distribution spatiale des espèces et les différentes variables environnementales étudiées est très faible. Certes, les semis et petites gaules d'érable et de hêtre ont une distribution indépendante dans l'espace, mais la distribution des deux espèces converge dans la classe de taille supérieure. La distribution et l'abondance des plus grosses gaules des deux espèces sont positivement corrélées et sont associées aux microsites où la croissance était élevée il y a une quinzaine d'années, ce qui est contraire au modèle conceptuel qui prédit une ségrégation spatiale des deux espèces. Il est proposé en discussion que l'étendue des conditions environnementales nécessaire à la coexistence stable de ces espèces ne soit pas suffisante à l'échelle locale.

Dans une seconde étude conduite à l'échelle régionale, nous avons testé trois hypothèses qui pourraient expliquer la recrudescence du hêtre, soit le lessivage des cations basiques du sol par les précipitations acides, l'éclaircissement de la voûte forestière par un épisode de dépérissement survenu dans la décennie 1980 et un changement de l'environnement lumineux du sous-étage associé à la succession secondaire. La structure d'âge des gaulis et le patron de croissance au fil du temps suggèrent des difficultés accrues de l'érable à sucre à se régénérer. Néanmoins, ces patrons ne correspondent pas aux prédictions faites par les deux premières hypothèses. Par contre, l'abondance relative de ces espèces parmi les gaules est étroitement associée à l'historique de petites perturbations des sites étudiés (ou du moins à la fréquence des épisodes de libération). Nous avons observé une diminution de la fréquence de ces petites perturbations au cours de la décennie 1980 suivie d'une augmentation de leur fréquence dans la décennie 1990. L'abondance relative de l'érable à sucre est négativement associée au creux de la décennie 1980 et à la reprise des annéés 1990. Ces résultats sont conformes au modèle traditionnel où l'abondance de ces espèces est principalement déterminée par la disponibilité de la lumière.

Les travaux empiriques présentés dans les deux premiers chapitres ont soulevé un certain nombre de questions fondamentales sur la dynamique de ces espèces. L'opposition des deux études quant à leur support du modèle conceptuel de coexistence de ces espèces proposé dans la littérature est la principale source de ce questionnement. Est-ce que ces espèces sont trop similaires pour que les subtiles différences mesurées soient suffisantes à leur coexistence? Est-ce que la stochasticité démographique élevée des gaulis est susceptible de contrer les différences entre les espèces? Quels sont les mécanismes qui assurent la coexistence de ces espèces? À quelle échelle spatiale doit-on considérer le modèle conceptuel? Ces questions sont abordées dans les chapitres suivants par l'étude de modèles de simulation théoriques.

Le troisième chapitre présente l'hypothèse d'un continuum entre les théories de la niche et neutre. L'effet de la différentiation des espèces sur la coexistence diminue avec la superposition des niches. Alternativement, l'augmentation de la similarité entre les espèces est accompagnée d'une progression de la stochasticité démographique. Pour des espèces similaires, la structure spatiale des populations, la dispersion et les phénomènes aléatoires qui peuvent affecter les populations auront un impact supérieur à la différentiation environnementale, et de ce fait la capacité de prédiction de l'abondance relative sera diminuée. Lorsque la variabilité dans la réponse de ces espèces à leur environnement est élevée, la dynamique est encore plus difficile à prédire. Ce sont aussi plusieurs mécanismes

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INTRODUCTION GÉNÉRALE

L'intérêt des écologistes forestiers pour la dynamique de l'érable à sucre (*Acer saccharum* Marsh.) et du hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) remonte au fondement de la discipline (Jones, 1946; Watt, 1947). Cette association d'espèces domine les forêts feuillues matures dans tout le nord-est de l'Amérique du Nord. Au Québec, on retrouve ces espèces en coexistence dans toute la zone tempérée (~ 110 000 km²). Mais au-delà de leur importance en termes de distribution géographique, l'intérêt des écologistes pour ces espèces vient du fait que leur coexistence est en apparente violation du principe d'exclusion compétitive (Woods, 1979). La similarité élevée de ces espèces très tolérantes à l'ombre par rapport aux autres espèces avec lesquelles elles compétitionnent dans leur aire de distribution en fait un cas très intéressant pour étudier les théories plus générales liées à la coexistence.

Comprendre les facteurs déterminant la distribution et l'abondance de ces espèces dans l'espace et dans le temps est un objectif qui a été longuement poursuivi, comme en fait foi l'imposante littérature sur le sujet. Des changements à court, moyen et long termes dans l'abondance relative de l'érable à sucre et du hêtre ont été couramment rapportés dans la littérature, certains en faveur de l'érable à sucre (Shanks, 1953; Ward, 1956; Siccama, 1971, McIntosh, 1972, Abrell et Jackson, 1977, Runkle, 1990; Fain *et al.* 1994; Poulson et Platt, 1996; Foré *et al.*, 1997; Cogbill, 2000; Brisson et Bouchard, 2003), d'autres en faveur du hêtre (Leak, 1970; Whitney, 1984; Brisson *et al.*, 1994; Beaudet *et al.*, 1999; Woods, 2000;; Forrester et Runkle, 2000 Duchesne *et al.*, 2005). Il est généralement reconnu que la composition de forêts matures dominées par des espèces tolérantes à l'ombre n'est généralement pas stable, même dans les forêts anciennes (Watt, 1947; Horn, 1975; Brisson *et al.*, 1994; Poulson et Platt, 1996; Woods, 2000).

Néanmoins, un consensus a semblé émerger récemment de la littérature sur une augmentation de l'abondance du hêtre et d'un échec de l'érable à sucre à se régénérer. Ce

problème écologique constitue un cas exemplaire pour étudier la dynamique de ces espèces et, plus généralement, pour mieux comprendre les phénomènes qui affectent les fluctuations d'abondance d'espèces en coexistence. Il existe dans la littérature des évidences de ce phénomène à de nombreux endroits dans l'aire de distribution de ces espèces (Ostrowsky and McCormack, 1986; Jenkins, 1997; Ray *et al.*, 1999; Schwarcz *et al.*, 2001; Forrester *et al.*, 2003; Hane, 2003; Duchesne *et al.* 2005; Angers *et al.*, 2005). À titre d'exemple, on a remarqué à la forêt de Hubbard Brook dans le New Hampshire que la densité des gaules de hêtre (< 10 cm au DHP) a augmenté de 5 fois de 1965 à 1997, alors que la densité des semis d'érable à sucre (< 50 cm de hauteur) a décliné de 20 fois et que la densité des petits gaulis (2-5 cm au DHP) a décliné de 80% (Hane, 2003). Ces observations sont confirmées également pour les Adirondacks (Jenkins, 1997). Des observations d'une abondance relative élevée du hêtre parmi les gaules ont été faites dans des forêts aménagées et anciennes (Brisson *et al.*, 1994 ; Schwarcz *et al.*, 2001; Angers *et al.*, 2005).

Le changement de la dynamique de recrutement est de deux ordres. Dans le sud du Québec, à la limite nord-est de l'aire de distribution de ces espèces, Duchesne *et al.* (2005) ont rapporté un déclin de 17% de la densité de l'érable de moins de 29.25cm au DHP dans les 10 dernières années, alors que la densité des gaules (1.1-9.0 cm au DHP) a doublé dans le même période. Ces résultats sont confirmés par l'analyse des inventaires forestiers du MRNQ. Alors que la densité des gaules de hêtre a presque doublé de la décennie 1980 à la décennie 1990 dans les forêts feuillues matures du sud du Québec, la densité des gaules d'érable est restée invariable durant cette période (Annexe). Il y a donc à la fois un changement d'abondance absolue pour le hêtre, ainsi qu'un changement de l'abondance relative.

Pour aborder ce phénomène et formuler des hypothèses de recherche, nous allons d'abord nous référer à un cadre théorique général sur la coexistence et ensuite à un modèle conceptuel de coexistence développé pour l'érable à sucre et le hêtre à grandes feuilles. Le cadre théorique est basé sur les récentes synthèses de Chesson (2000a) et de Adler *et al.* (2007). Le modèle conceptuel de coexistence quant à lui se base sur les travaux empiriques de Forcier (1975), Canham (1988, 1990), Poulson et Platt (1996) ainsi que de Arii et Lechowicz (2002). Par la suite, les objectifs et la structure de la thèse seront présentés.

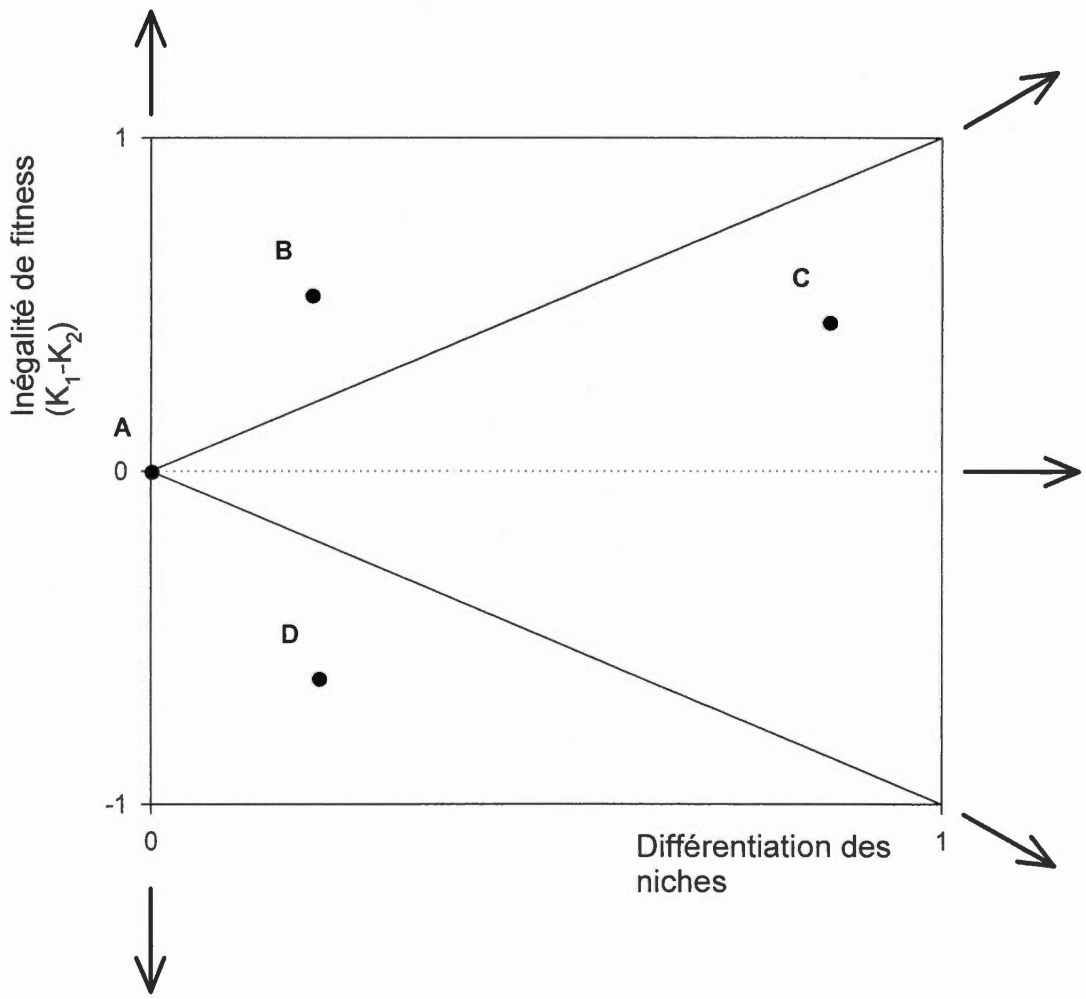
I.1 La théorie de la coexistence

La coexistence est définie très simplement dans le dictionnaire Robert par « *l'existence simultanée* ». L'usage courant du terme coexistence dans la littérature écologique est très similaire à cette définition. Généralement, le terme coexistence est employé pour signifier la présence stable dans le temps de deux ou plusieurs espèces au sein d'une même communauté. Cette définition se distingue cependant par la précision des dimensions temporelle et spatiale. Cette définition est néanmoins générale et les théoriciens en ont une beaucoup plus précise. On distingue la coexistence stable de la coexistence instable. La coexistence stable signifie que la densité des espèces dans une communauté est constante à long terme, et que si la densité d'une espèce devient faible, elle tend à remonter (Chesson, 2000a). Mathématiquement, cette définition correspond à un taux de croissance positif en situation de rareté pour chacune des espèces qui coexistent, soit le critère d'invasibilité (MacArthur et Levins, 1967). La coexistence instable se rapproche de l'usage courant du terme, signifiant que les espèces de la communauté ne peuvent récupérer suite à des périodes à faible abondance et que l'existence simultanée dans une communauté est strictement transitoire.

Pourquoi la coexistence est-elle un problème d'intérêt pour les écologistes? Considérons l'ensemble des espèces d'arbres que l'on retrouve sur la terre. Pourquoi chaque espèce est-elle absente de la plupart des environnements? Une fois que l'on élimine les contraintes historiques et de tolérance environnementale, le principal facteur qui limite la diversité est la compétition (Zobel, 1992). Ce raisonnement tire son origine du principe d'exclusion compétitive qui se résume ainsi: deux espèces similaires qui compétitionnent simultanément pour les mêmes ressources ne peuvent coexister sur un même site; si elles ne se différentient pas d'une certaine manière, l'une des espèces deviendra éventuellement dominante et éliminera l'autre (Gause, 1934). Un mécanisme de coexistence se définit par conséquent comme un processus écologique qui empêche l'exclusion compétitive de se réaliser et permet de maintenir la diversité au sein d'une communauté.

Chesson (2000a) a proposé un cadre théorique général qui permet de catégoriser les mécanismes de coexistence. Ce cadre théorique est illustré à la figure I.1 (d'après l'interprétation de Adler *et al.*, 2007). Pour aider à le comprendre, considérons la dérivation mécanistique du modèle Lotka-Volterra par MacArthur (MacArthur, 1970; Chesson, 2000a).

Figure I.1 Illustration des conditions pour assurer la coexistence stable entre deux espèces (d'après Adler et al., 2007). En abscisse se trouve l'effet du terme de stabilisation (le terme de droite dans l'équation 1) et en ordonnée le terme d'inégalité (terme de gauche dans l'équation 1) calculé entre les espèces 1 et 2. Lorsque les deux espèces sont équivalentes et qu'il n'y a pas de différences de niches, on se trouve à un point neutre (A). Au point B, l'espèce 1 exclut l'espèce 2 parce qu'elles ne sont pas différentiées suffisamment et que l'espèce 1 a un fitness plus élevé, alors qu'au point D, la différence de fitness est favorable à l'espèce 2. Il y a coexistence stable au point C. Les flèches indiquent une accélération du taux de succession (l'inverse du temps pour atteindre l'équilibre).



Eq. 1 $$\overline{r_i} = b_i(k_i - k_s) + b_i(1-\rho)k_s$$

Le taux de croissance moyen à long terme d'une espèce i lorsqu'elle est à faible abondance, $\overline{r_i}$, se définit par deux termes : une différence de fitness auquel s'additionne un terme de stabilisation. La différence de fitness est ici exprimée par la différence de capacité de support k de l'espèce rare *i* par rapport à l'espèce *s*, multipliée par le taux de croissance en absence de compétition, b_i. Cette différence de fitness s'évalue pour l'environnement moyen de la communauté où se situent les espèces. Le terme de stabilisation dépend fortement de la superposition des niches, □. À tout moment lorsque □ est inférieur à 1, le terme de stabilisation est positif et il contribue à la croissance de l'espèce rare. Il est nul en absence de différentiation et positif lorsque les niches se distinguent. Plus les espèces sont différentiées dans leur usage de l'environnement (plus petit est □), plus le terme de stabilisation est élevé.

Si l'on considère le cas simple de deux espèces et que l'on place en abscisse le terme de stabilisation et en ordonnée la différence de fitness entre les deux espèces, trois régions se définissent (figure I.1). Dans les régions supérieure et inférieure, le terme de stabilisation n'est pas assez élevé pour compenser la différence entre les espèces et il y a exclusion compétitive. Le principe d'exclusion compétitive correspond à la situation où le terme de stabilisation est nul et qu'il y a inégalité entre les espèces. Le cas extrême où à la fois les termes d'inégalité et de stabilisation sont nuls correspond à une dynamique neutre (définie brièvement plus loin). La magnitude du terme de stabilisation nécessaire à la coexistence stable dépend de la différence de fitness entre les espèces. Par ailleurs, en plus de définir les conditions requises pour la coexistence, la combinaison des termes d'inégalité et de stabilisation définira également le taux de succession des espèces au sein de la communauté lorsque la composition est momentanément déplacée de son équilibre.

Les mécanismes de coexistence sont les processus écologiques qui affectent les termes d'inégalité et de stabilisation. Chesson (2000a) distingue donc les mécanismes d'égalisation et les mécanismes de stabilisation. Notons que seuls les mécanismes de stabilisation permettent la coexistence stable. Néanmoins, comme mentionné précédemment, un mécanisme d'égalisation peut favoriser la coexistence si le terme de stabilisation est faible.

Les mécanismes de stabilisation sont intuitifs pour la plupart des écologistes; ils correspondent à toute forme de différentiation des niches, que ce soit en terme d'habitat ou d'utilisation de la ressource (Chase et Leibold, 2003). La niche peut être associée à l'utilisation spécifique de ressources, ou bien à l'hétérogénéité spatiale ou temporelle de l'environnement (e.g. le « storage effect », Chesson et Warner, 1981). Les mécanismes d'égalisation sont plus subtils. Les processus associés à la dispersion limitée (Hurtt et Pacala, 1995) et à la structure spatiale du paysage (Mouquet et Loreau, 2002), par exemple, affecteront le terme d'inégalité. La prédation, lorsqu'elle n'est pas densité-dépendante, pourrait également être considérée comme un mécanisme d'égalisation.

Au chapitre des communautés forestières, de très nombreuses hypothèses ont été proposées pour expliquer la coexistence. Celles qui sont les plus couramment véhiculées comprennent la niche de régénération (Grubb, 1977), le remplacement réciproque (Fox, 1977; Woods, 1980), la spécialisation pour la lumière dans un environnement rendu hétérogène par la formation de trouées (Ricklefs, 1977; Denslow, 1980), l'hypothèse du ratio de ressources (Tilman, 1982), un compromis entre la compétitivité et les capacités de colonisation (Tilman, 1994), une dispersion limitée qui réduit la compétition (Hurtt et Pacala, 1995), l'hypothèse des perturbations intermédiaires (Connell, 1978) et la densité-dépendance négative (Janzen, 1970; Connell, 1971). Ces hypothèses ne sont cependant pas formulées de façon à pouvoir être explicitement intégrées au cadre de Chesson (2000a), même que bien souvent les mécanismes de coexistence qui sous-tendent les hypothèses ne sont pas identifiés (e.g. Roxburgh *et al.*, 2004).

Finalement, dans le cas extrême où l'inégalité entre les espèces et le terme de stabilisation sont nuls se trouve une dynamique neutre (Hubbell, 1997; 2001; Bell, 2000). Le modèle neutre est la plus simple représentation de la dynamique de communautés. Les processus inclus au modèle sont la reproduction, la mortalité, l'immigration et la spéciation. Le modèle assume simplement que les espèces sont écologiquement équivalentes, indépendamment des caractéristiques de l'environnement. En y combinant de la stochasticité démographique, chaque espèce est invariablement destinée à une lente marche aléatoire vers l'extinction. Dans une communauté locale, la coexistence est transitoire, mais la diversité est maintenue par une balance entre l'extinction et l'immigration. L'immigration assure

néanmoins une certaine stabilité à la composition locale au sens de Chesson (2000a). Les modèles neutres sont très efficaces pour prédire de nombreux patrons macroécologiques (Bell, 2001; Hubbell, 2001; McGill, 2003a; Volkov *et al.*, 2003). Une version différente du modèle neutre basée sur la densité-dépendance négative s'est également avérée très performante à prédire les distributions d'abondance relative (Volkov *et al.*, 2005). Bien que très puissants et parcimonieux, ces modèles suscitent cependant énormément de controverse (Whitfield, 2002; Harte, 2003; Nee et Stone, 2003; McGill, 2003b, Gaston et Chown, 2005; Gewin, 2006). Le plus souvent, lorsque l'on effectue des tests d'hypothèses plus élaborés que de simples évaluations de la correspondance de patrons, la théorie n'est pas supportée du tout, ou alors seulement partiellement par les données de terrain (e.g. Clark et McLachlan, 2003; Fargione *et al.*, 2003; Uriarte *et al.*, 2004; Gilbert et Lechowicz, 2004; Adler, 2004; Harpole et Tilman, 2005; Wootton, 2005).

I.2 La coexistence de l'érable et du hêtre

Maintenant que nous avons brièvement dressé un cadre théorique pour comprendre les mécanismes qui affectent la coexistence, nous pouvons nous questionner sur la dynamique de l'érable à sucre et du hêtre à grandes feuilles. Bien que les différents modèles de coexistence proposés pour ces espèces puissent être interprétés à l'aide du cadre de Chesson (2000a), cela n'a jusqu'à présent pas été fait de façon formelle, suite à un développement théorique rigoureux.

L'érable à sucre et le hêtre à grandes feuilles sont deux espèces très tolérantes à l'ombre comparativement à l'ensemble des espèces d'arbres avec lesquelles elles coexistent dans les forêts du nord-est américain (à l'exception de la pruche - Baker, 1949). Même si ces deux espèces peuvent survivre plus de 100 ans sous le couvert de forêts matures (Canham, 1990), une disponibilité très réduite de la lumière serait susceptible de causer un stress supérieur à l'érable à sucre qu'au hêtre (Beaudet *et al.*, 1999). La mortalité de l'érable à sucre est en effet plus élevée que celle du hêtre sous des conditions de très faible disponibilité lumineuse (Kobe *et al.*, 1995; Beaudet *et al.*, 1999; Caspersen et Kobe, 2001). La lumière étant généralement le facteur le plus limitant dans les forêts où ces espèces coexistent (Beaudet *et al.*, 1999), le cadre théorique décrit précédemment prédit que le hêtre devrait éventuellement exclure l'érable à sucre dans un environnement uniforme. La question est

donc de savoir quels sont les mécanismes et traits de vie qui contribuent à la coexistence de ces deux espèces, soit par différentiation ou stabilisation.

L'érable à sucre et le hêtre diffèrent sur la base de plusieurs traits de vie. Les études s'accordent à dire que le hêtre a la croissance radiale et en hauteur la plus élevée à faible lumière, mais dans les trouées ou les environnements plus lumineux, certaines études placent l'érable comme l'espèce gagnante (Bicknell, 1982; Bellefleur et Larocque, 1983; Canham, 1988; 1990; Poulson et Platt, 1996; McClure *et al.*, 2000), alors que d'autres placent le hêtre égal ou supérieur (Cypher et Boucher, 1982; Pacala *et al.*, 1994; Beaudet et Messier, 1998; Finzi et Canham, 2000; Arii, 2002; Beaudet *et al.*, sous presse). La performance relative de ces espèces sous de faibles conditions de lumière serait cependant affectée par les propriétés du sol, l'érable à sucre ayant une mortalité plus élevée sur les sites pauvres en calcium (Kobe, 1996; Kobe *et al.*, 2002; Juice *et al.*, 2006) et le hêtre sur les sites secs (Caspersen et Kobe, 2001). Cette différentiation expliquerait la ségrégation spatiale de la régénération et des adultes qui a été observée dans de nombreuses études (van Breemen *et al.*, 1997; Finzi *et al.*, 1998; Woods, 2000; Arii et Lechowicz, 2002).

L'érable et le hêtre diffèrent également à d'autres stades de vie qu'au stade juvénile. Le hêtre produit de nombreux drageons lorsque les racines sont blessées ou exposées à l'air (Jones et Raynal, 1987; 1988). Ceux-ci ont souvent une meilleure survie et croissance que les semis (Beaudet *et al.*, 1999; Arii, 2002; Beaudet *et al.*, manuscrit non publié). La dispersion des graines et des drageons chez le hêtre est cependant beaucoup plus limitée que celle des graines de l'érable à sucre (Jones et Raynal, 1986; Ribbens *et al.*, 1994). La fécondité de l'érable à sucre est également beaucoup plus élevée (Graber et Leak, 1992) et les graines du hêtre subissent une intense prédation par les oiseaux, petits mammifères et insectes (Graber et Leak, 1992). Finalement, le hêtre serait sensible à une grande variété de pathogènes susceptibles d'affecter sa longévité (Burns et Honkala, 1990). Cela pourrait rendre les hêtres adultes plus sensibles que les érables à sucre à des perturbations comme le verglas (Rhoads *et al.*, 2002) et les tempêtes de vent (Papaik et Canham, 2006).

De nombreux modèles conceptuels ont été proposés pour expliquer la coexistence de l'érable et du hêtre, à commencer par celui de Forcier (1975). Cet auteur a introduit l'idée que

la coexistence du bouleau jaune, de l'érable à sucre et du hêtre serait le résultat de micro-successions à l'intérieur d'une communauté, celles-ci étant initiées par la formation de petites trouées. L'abondance de chacune des espèces serait stable à l'échelle de la communauté, malgré des oscillations entre les trois espèces à une échelle spatiale plus restreinte (e.g., quelques arbres). Le modèle mise sur les petites perturbations ainsi que sur l'existence d'une stricte hiérarchie entre les espèces au niveau de leur tolérance à l'ombre et de leurs capacités de dispersion. Ce modèle a été généralisé par Tilman (1994) sous le nom de « competition/colonization trade-off ».

Le modèle de Forcier (1975) a par la suite été précisé par Canham (1988; 1990) et Poulson et Platt (1996). Ces derniers se sont concentrés sur la dynamique de l'érable et du hêtre, et particulièrement sur leur différente réponse à la disponibilité de la lumière. Essentiellement, les deux espèces coexistent en vertu d'une course presque neutre dans leur accès à la canopée. L'érable à sucre survit relativement bien aux périodes de suppression mais sa croissance y est faible, alors que le hêtre y survit très bien et poursuit sa croissance. Au moment de la formation de trouées, la réponse de l'érable à sucre en croissance sera selon ces auteurs largement supérieure à celle du hêtre, ce qui lui permettra de profiter davantage de la lumière disponible à ce moment. La fréquence et la durée des périodes de suppression et de libération déterminera l'espèce qui parviendra la première à la canopée ainsi que le nombre d'individus qui y accèderont. Le régime de formation de petites trouées (en intensité et fréquence) affectera à terme la balance entre les deux espèces. Sous ce modèle, la coexistence résulte d'une spécialisation dans le temps et l'espace de l'utilisation de la lumière.

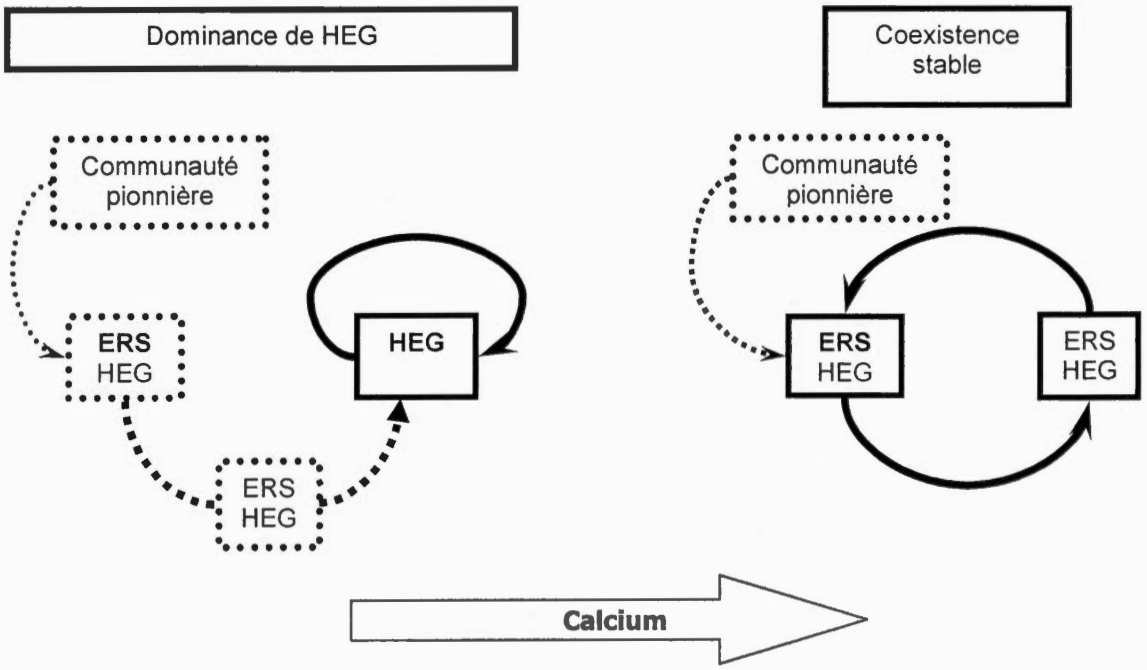
Le modèle est complété par l'ajout de l'hétérogénéité spatiale du sol (Arii et Lechowicz, 2002). Le modèle que nous proposons est illustré à la figure I.2. Les propriétés du sol varient naturellement dans l'espace à l'intérieur de la communauté (van Breemen *et al.*, 1997) et les espèces affectent la disponibilité des nutriments (Finzi *et al.*, 1998; Dijkstra *et al.*, 2001; 2002). Plus spécifiquement, le hêtre tend à acidifier le sol dans son voisinage (Dijkstra *et al.*, 2001), alors que l'érable augmente la disponibilité du calcium (Dijkstra *et al.*, 2002). Il s'en suit un effet de rétroaction positive de chacune des espèces à leur présence qui permettra aux deux espèces de se spécialiser à différents endroits dans l'espace. Sur les

microsites les plus pauvres, parce que l'érable ne devrait pas être en mesure de survivre dans les conditions les plus sombres, on devrait s'attendre à une succession en faveur du hêtre. La position d'une communauté au long de la sère successionnelle devrait déterminer l'abondance relative des deux espèces. Avec l'amélioration de la fertilité du sol, sur les microsites les plus riches, on devrait progressivement voir le régime de formation de petites trouées être le principal facteur affectant l'abondance relative des espèces (comme le suggère le modèle de Poulson et Platt, 1996).

La dispersion limitée du hêtre est susceptible d'interférer sur cette dynamique. La dispersion limitée est un mécanisme égalisateur qui ralentit la dynamique d'exclusion par l'espèce supérieure et qui facilite la coexistence. Les processus qui favoriseront une distribution spatiale agrégée, comme des perturbations (Wooton, 2001), devraient donc être favorables à l'érable à sucre. Ce mécanisme sera d'autant plus efficace dans ce système considérant que les drageons du hêtre, plus performants que les semis, ne seront produits que par des hêtres matures. La différence de compétitivité entre l'érable et le hêtre est donc susceptible de s'accroître de façon non linéaire (rétroaction positive) avec la densité du hêtre parmi les adultes.

Dans ce modèle, l'érable à sucre évite l'exclusion compétitive par deux mécanismes de différentiation au stade de recrutement, rendus possibles grâce à l'hétérogénéité 1) spatiale et temporelle de la lumière créée par la formation de petites trouées dans la voûte forestière et 2) spatiale de l'environnement édaphique à l'intérieur du peuplement. Il s'agit d'une dynamique non équilibrée, mais stabilisée par des mécanismes de coexistence. Le modèle repose sur l'hétérogénéité environnementale à une échelle qui correspond à celle où s'effectue la compétition pour le recrutement à la canopée, soit approximativement l'échelle de la trouée. De l'hétérogénéité spatiale structurée à une échelle inférieure à celle où s'opère les interactions compétitives sera équivalente à un environnement uniforme, de même que de l'hétérogénéité structurées à une échelle spatiale supérieure à celle de la communauté.

Figure I.2 Illustration schématique du modèle conceptuel de coexistence pour l'érable à sucre (ERS) et le hêtre (HEG). Les caractères gras signifient la dominance. Les lignes pointillées représentent la succession, alors que les lignes pleines représentent le remplacement au sein de la communauté climacique.



I.3 Objectifs

Il y a deux objectifs généraux qui sont poursuivis dans cette thèse. D'abord, au terme de cette thèse nous devrions être en mesure de décrire la dynamique de l'augmentation récente du hêtre parmi les gaules et d'avoir testé les principales hypothèses sur son origine (action des précipitations acides, dépérissement des érablières et succession forestière). En second, par l'étude de ce phénomène et par des études théoriques, nous devrions être en mesure de mieux comprendre les mécanismes qui permettent la coexistence et affectent la dynamique d'espèces forestières très tolérantes à l'ombre.

I.4 Structure de la thèse

Cette thèse est constituée de six chapitres présentés sous la forme d'articles scientifiques. La thèse est unie par un thème commun : la stabilité (sensu Chesson, 2000a) de la coexistence en fonction de la similarité des espèces et de l'hétérogénéité environnementale. Les deux premiers chapitres sont empiriques et ils portent spécifiquement sur la distribution spatiale et l'abondance de l'érable à sucre et du hêtre. Les quatre chapitres suivants sont théoriques, développés à partir de modèles de simulation, et leurs résultats sont généralisables à une grande variété de communautés d'organismes sessiles. Ces chapitres théoriques sont destinés à compléter la connaissance théorique nécessaire à l'interprétation des résultats observés dans les premiers chapitres.

Au premier chapitre, nous nous interrogeons sur la capacité du modèle conceptuel de coexistence présenté plus haut à prédire la distribution spatiale de la régénération d'érable et de hêtre dans une communauté mésique et mature. Cette hypothèse est une construction logique basée sur la réponse fonctionnelle de ces espèces à différentes variables environnementales, mais elle n'a pas été testée explicitement à l'échelle de la communauté. Dans ce chapitre, nous testons si les caractéristiques de l'environnement permettent de prédire la variabilité spatiale de la régénération dans une communauté où l'érable et le hêtre coexistent.

Au second chapitre nous poursuivons le test du modèle conceptuel de coexistence de l'érable à sucre et du hêtre. Cette fois-ci, le modèle est employé pour générer des hypothèses sur les causes possibles de l'augmentation récente du hêtre dans le sous-étage des érablières

au Québec. L'analyse porte donc sur les facteurs qui affectent la distribution de l'érable et du hêtre à l'échelle régionale. Nous identifions trois changements environnementaux majeurs survenus à l'échelle régionale et susceptibles d'affecter la dynamique de régénération : 1) le lessivage des cations basiques du sol par les précipitations acides; 2) l'éclaircissement de la cime par l'épisode de dépérissement des érablières qui est survenu dans les années 1980 et 3) la succession secondaire.

Les deux premiers chapitres ont soulevé un certain nombre de questions pour lesquelles ni le cadre théorique de Chesson (2000a) ni le modèle conceptuel de coexistence ne procurait de réponses. Les chapitres suivants sont donc des développements théoriques destinés à améliorer la compréhension de ces résultats, et plus généralement, de la dynamique d'espèces forestières similaires.

L'érable à sucre et le hêtre à grandes feuilles sont deux espèces très similaires écologiquement, mais pas nécessairement équivalentes. Au troisième chapitre, nous nous posons la question : à quel point deux espèces doivent-elle être similaires pour que la dynamique devienne neutre? Stabilisée? Et quelle est l'interaction avec la dispersion limitée? Autrement dit, nous poursuivons l'objectif de développer l'hypothèse d'un continuum de la théorie neutre à la théorie de la niche. Les hypothèses sont que des processus neutres et de stabilisation structurent simultanément les communautés et que l'importance relative de ces processus varie au long d'un continuum.

Les travaux poursuivis au troisième chapitre rendent nécessaires le développement de méthodes pour quantifier la « neutralité » d'une communauté. Borcard *et al.* (1992) ont développé un cadre méthodologique pour partitionner la variabilité spatiale dans la composition de communautés entre des fractions environnementales et spatiales. Ce cadre méthodologique a été maintes fois utilisé pour quantifier la neutralité d'une communauté. Au quatrième chapitre, nous démontrons que cette approche est erronée pour de nombreuses raisons. En utilisant une approche alternative qui tient compte explicitement des processus de dispersion limitée (neutre) et de différentiation environnementale (niche), nous démontrons l'importance de modéliser ces processus de façon mécanistique plutôt que phénoménologique. Cette approche permet aussi de vérifier l'hypothèse avancée au troisième

chapitre où il est proposé que les communautés sujettes à la dispersion limitée sont constituées d'un agencement d'espèces complémentaires et stables et d'espèces redondantes et transitoires.

Le cadre théorique de Chesson (2000a), tout comme le modèle conceptuel de coexistence, assument une réponse déterministe des espèces à leur environnement et à la compétition. Trop souvent, les écologistes confondent le test de différence statistique entre deux espèces sur un paramètre donné avec un test d'hypothèse biologique. Une fois qu'un test statistique a révélé une différence significative entre les espèces, on assume que cette différence est suffisante pour la coexistence. La théorie de la limite à la similarité de MacArthur et Levins (1967) prédit qu'une différence minimale entre les espèces est nécessaire pour leur coexistence stable. Cette théorie est confirmée en présence de stochasticité démographique par Tilman (2004) et le chapitre 3. L'objectif du chapitre 5 est de comprendre comment la différence minimale nécessaire entre les espèces pour qu'il y ait coexistence est affectée par de la stochasticité dans la réponse des espèces à leur environnement. Nous posons l'hypothèse que la variabilité entre les individus au sein d'une espèce va augmenter la stochasticité démographique et donc la dérive aléatoire. Nous posons également l'hypothèse que la variabilité temporelle de réponse au sein d'un individu, lorsqu'elle covarie entre les espèces, va résulter en un effet stabilisateur en vertu de l'effet de « storage ».

Finalement, nous concluons la thèse au chapitre 6 par une étude sur les mécanismes de coexistence en forêt basés sur le compromis entre la croissance en trouées et la survie en sous-couvert. Il est généralement admis que l'hétérogénéité spatio-temporelle de la disponibilité de la lumière créée par la formation de petites trouées, combinée à la différentiation des espèces dans leur tolérance à l'ombre, permet de maintenir une grande diversité d'espèces forestières en coexistence. Le modèle conceptuel de coexistence de l'érable à sucre et du hêtre est basé sur cette hypothèse. Néanmoins, il n'y a jamais eu de développement théorique formel et rigoureux pour identifier les mécanismes de coexistence impliqués dans cette hypothèse. Au sixième chapitre, nous poursuivons l'objectif d'identifier ces mécanismes de coexistence. Assisté de la théorie de coexistence de Chesson (1994, 2000b) dans les environnements variables, nous identifions deux mécanismes de coexistence:

la non-linéarité relative et l'effet de « storage ». Nous utilisons la théorie générale et un modèle de simulation spécifique aux communautés forestières pour élaborer une série de prédictions sur comment l'espace de paramètre du compromis croissance/survie doit varier avec l'hétérogénéité environnementale (spatiale et temporelle) et la dispersion limitée.

CHAPITRE I

FACTORS AFFECTING SAPLING SPATIAL DISTRIBUTION IN A SUGAR MAPLE-BEECH UNEVEN-AGED COMMUNITY

Dominique Gravel, Marilou Beaudet, Christian Messier

1.1 Résumé

La communauté de l'érable à sucre et du hêtre à grandes feuilles est un système typique pour étudier la coexistence d'espèces forestières très tolérantes à l'ombre. Un modèle conceptuel de coexistence a été proposé, basé sur un compromis entre la survie à faible lumière et la croissance à forte lumière et son interaction avec la fertilité du sol. L'objectif de cette étude est de tester si les caractéristiques de l'environnement (lumière, sol, historique de croissance) permettent effectivement de prédire la variabilité spatiale de l'abondance relative des gaules d'érable à sucre et de hêtre dans une communauté où ces espèces coexistent. Une prédiction supplémentaire du modèle conceptuel est que la distribution spatiale des semis sera essentiellement limitée par la dispersion, alors qu'avec une progression de la taille, ce sera l'environnement qui sera davantage limitant et donc le principal déterminant des patrons de distribution des gaules. Pour tester ces prédictions, nous avons réalisé un échantillonnage détaillé dans une parcelle de 0.24 ha (sur une grille de quadrats de 25m²) dans une communauté mature d'érable et de hêtre. Les caractéristiques du sol, la disponibilité de la lumière et l'historique de croissance radiale ont été finement mesurés pour modéliser la distribution spatiale des gaulis pour différentes classes de taille. Les résultats présentés dans cette étude montrent que l'abondance relative des semis et gaulis est effectivement partiellement associée aux caractéristiques de l'environnement. Un examen approfondi des données révèle cependant que les relations entre la composition en espèces et les variables environnementales sont faibles et souvent fortuites. Les variables sélectionnées pour modéliser la distribution des espèces changent effectivement avec la taille, mais pas d'une manière cohérente. Dans l'ensemble, les résultats ne supportent pas le modèle conceptuel de coexistence. Il est proposé dans la discussion que, en raison de la similarité de ces espèces et de la stochasticité démographique élevée, le modèle conceptuel ne permettrait probablement de prédire la distribution des espèces qu'à des échelles spatiales supérieures. À l'échelle locale, la dynamique serait plutôt neutre, ou du moins transitoire.

Mots clés: Érable à sucre, hêtre à grandes feuilles, coexistence, analyse spatiale, hétérogénéité spatiale, dispersion

1.2 Abstract

The association of sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) is a typical system for the study of coexistence among highly shade tolerant species. A conceptual model of coexistence was proposed, based on a low light survival/high light growth trade-off and on its interaction with soil fertility. The objective of this study is to test if environmental characteristics (light, soil, growth history) are good predictors of spatial variation in relative abundance of maple and beech saplings within a community where they co-occur. A further prediction of this conceptual model of coexistence is that seedling distribution will be mostly dispersal limited and that impacts of environmental limitation on the spatial distribution will increase with size. In order to test these predictions, we performed a detailed sampling over a grid of 25m² quadrats in a 0.24 ha mature maple-beech community. Soil characteristics, light availability and growth history were finely measured to model sapling composition across different size classes. Results presented here show that species abundance is somewhat related to the environmental characteristics. A close examination of the data show the significant relationships between species relative abundance and environmental characteristics are weak and might be spurious. The variables selected to model species distribution do effectively change with size, but not coherently with the conceptual model. Overall, results are not supportive of the conceptual model of coexistence. It is proposed that, because of the high similarity of these species and of elevated demographic stochasticity, that this conceptual model can only predict species distribution at larger spatial scales. At the local scale, coexistence would rather be neutral, or at the very least, transient.

1.3 Introduction

The explanation of coexistence of highly shade tolerant tree species is a longstanding challenge for forest ecologists. There are some theoretical evidences (Chesson, 2000a) suggesting that only a small amount of niche differentiation would be necessary to compensate for the small fitness inequality of shade tolerant trees. There is a long list of life history strategies allowing such differentiation, including negative density dependence (the Janzen-Connell effect, see a review by Wright, 2002), the regeneration niche (Grubb, 1977), the presence of a differentiated response to canopy gaps (Pacala et al., 1996; Chapter 6) and the competition-colonization trade-off (Tilman, 1994). Others would argue that when species are so similar in their life history strategies, demographic stochasticity would dominate the dynamics and coexistence would be transient because of the slow turnover rate of forest communities (Chapters 3, 5; Scheffer and van Ness, 2006; Holt, 2006). Limiting similarity would even be amplified when species response to their environment is variable (Chapter 5).

The dynamics of sugar maple and American beech is a typical example for studying coexistence of highly shade tolerant species. A conceptual model of coexistence was first proposed by Forcier (1975) and further developed by Canham (1988, 1989), Poulson and Platt (1996) and Arii and Lechowicz (2002). Sugar maple and American beech are two highly shade tolerant species (Baker, 1949) that can survive long periods of suppressed growth (Canham, 1990; Chapter 2). American beech is however slightly more tolerant to shade because of higher survival and growth under low light conditions (Canham, 1988; Kobe et al., 1995; 2002). The higher shade tolerance of American beech is more pronounced for saplings of root sprout origin (Forcier, 1975; Beaudet et al., 1999). On the other hand, sugar maple usually grows faster than beech in high light conditions (Bicknell, 1982; Bellefleur and Larocque, 1983; Canham, 1988; 1990; Poulson and Platt, 1996; McClure *et al.*, 2000), although there are evidence that this hierarchy is quite variable (Cypher et Boucher, 1982; Pacala *et al.*, 1994; Beaudet and Messier, 1998; Finzi and Canham, 2000; Arii, 2002; Beaudet *et al.*, in press).

The conceptual model that emerged from the above-cited studies states that coexistence occurs because of an asynchronous race for recruitment to the canopy (Canham, 1989, 1990). There is now theoretical evidence that the high light growth/low light survival

trade-off is sufficient to allow stable coexistence of two species in the presence of temporal variability in light availability (Chapter 6). The conceptual model predicts that species relative abundance will vary along the micro-succession initiated by a canopy gap (Forcier, 1975; Poulson and Platt, 1996) and vary with canopy gap history (Poulson and Platt, 1996). Variation in species relative abundance is further thought to be affected by an interaction of survival with soil properties. Base cations and water availability are factors respectively affecting the low light survival of maple (Kobe et al., 1995; 2002) and beech (Caspersen and Kobe, 2001). Since soil properties tend to be spatially heterogeneous because of the natural variability of the mineral content (van Breemen et al., 1997) and soil-plant interactions (Dijkstra et al., 2001; 2002), it is believed that these life-history traits further contribute to the coexistence of these species (Chapter 6; Finzi et al., 1998; Arii and Lechowicz, 2002; Canham et al., 2006).

The conceptual model of coexistence described above is, however, mostly based on the interpretation of species life history traits. The model must be validated because we might erroneously interpret species statistical differentiation as evidence of niche differentiation allowing stable coexistence (Chapter 5). It is clear that the above relationships are quite variable from stem to stem and from site to site (see for instance Kobe, 1996). One approach to test the model would be to measure the species demographic response to a disturbance. The model predicts a shift in relative abundance in favour of sugar maple following small-scale disturbance. This test of the model has been performed recently in an old-growth forest disturbed by an intense ice storm (Beaudet et al., in press). Seven years after the ice storm, once the light conditions had returned to their pre-disturbance levels, the authors did not observe any substantial shift in species relative abundance in any regeneration size class.

Another test of the conceptual model would be to determine how sapling relative abundance, a proxy of recruitment success, varies as a function of the environment and the local disturbance history. It is particularly important to conduct such an analysis at the local scale (~25m², the area covered by the crown of a mature tree), with the range of environmental conditions susceptible to allow coexistence of these species in a forest community. Numerous observational studies were conducted at larger spatial scales (e.g.

Woods, 2000; Arii and Lechowicz, 2002; Chapter 2), where environmental gradients could be strong, but these scales do not match the one at which competitive interactions occur.

The objective of this study is to test if environmental characteristics (light and soil properties) are good predictors of spatial variation in the relative abundance of sugar maple and beech seedlings and saplings within a community where they co-occur. The conceptual model predicts the composition of the small size classes will be better predicted by the seed rain, light availability and soil fertility, while the past light availability (here approximated by growth history) and soil fertility will better predict larger sapling abundance. A further prediction is that new year seedling distribution will be mostly neutral (dispersal limited) and that impact of environmental limitation on the spatial distribution will increase with size (a proxy of age). In order to test these predictions, we performed a detailed sampling over a grid of 25m² quadrats in a 0.24 ha mature sugar maple-beech community. Soil characteristics, light availability and radial growth history were measured to model saplings composition across different size classes.

1.4 Methodology

1.4.1 Study Site

The study site is located at the Duchesnay forest Station (46°70'-47°00'N, 71°35'-71°45'W), 50 km north of Quebec City. The vegetation of the station is dominated by mature deciduous forest stands with patches of mixed and coniferous stands. The mean annual temperature is 3.4°C and the mean annual precipitation is 1300 mm (Houle et al., 1997). A mature forest stand was selected based on representative conditions where the maple-beech community is found. The stand is located at mid-slope, on a thick glacial till deposit, well to moderately well drained. The location of the sampling plot was arbitrarily chosen to ensure the presence of sufficient within-plot heterogeneity, based on micro-topography, in order to assure spatial variations in soil properties. The composition of the cover (trees >9.1 cm at DBH) is dominated by sugar maple (55.9% of basal area), American beech (27.0%), *Betula alleghaniensis* Britton (15.7%), with presence in the stand surrounding the plot of *Acer rubrum* L., *Acer pensylvanicum* L., *Tsuga canadensis* (L.) Carr., *Abies balsamea* (L.) Mill., and *Picea rubens Sarg*. The total basal area was 24.9 m²/ha and the largest diameter recorded

in the plot is 71.1 cm. The most common herbaceous and shrub species were *Lycopodium lucidulum*, *Dryopteris spinulosa*, *Streptopus roseus*, *Trillium erectum*, *Oxalis Montana*, *Clintonia borealis and Taxus canadensis*. Signs of beech bark disease were present, but at the time of the study the disease appeared to have no significant effect in this forest. The stand could have been subjected to partial harvest prior to the 1950s, as most stands in the region, but there was no evidence of past disturbance on the site, and understory saplings of maple and beech between 100 and 200 years old were previously found at this site (Chapter 2).

1.4.2 Field sampling

Spatial coordinates, DBH and species identity was recorded for every tree larger than 4.1 cm at DBH in a 75 X 125m plot. A more intensive sampling was conducted in a 30 X 80m subplot centered in the plot, divided in a grid of 5 X 5m quadrats. For every quadrat, we recorded every sapling between 1m height and 4.0cm DBH. New year seedlings (with cotyledons) density was measured in a 1m² subplot centered on the quadrat. Density of seedlings up to 1m height was measured in a 2 m radius (12.57 m²) subplot centered on the quadrat. Light availability was determined at the center of each quadrat, at 1 and 4m above-ground by measuring the photosynthetic photon flux density (PPFD) with a light sensor (LI-190SA point quantum sensor, LICOR, Lincoln, NE, USA) and expressed as the percentage of the PPFD measured simultaneously with a sensor located in a open area less than 250 m from the study site. Measurements were taken under a cloudy sky following the method of Parent and Messier (1996). One soil sample was taken at the center of the quadrat and combined to three other samples located on opposite directions at 1 m from the center of the quadrat. Sampling was done on the first 5 cm of the B horizon. Finally, a disk was sampled at 20 cm height on one sapling per quadrat. Saplings growth history is used as a proxy of past light availability (Chapter 2). The selected sapling was preferentially a beech (easier to read and less ring anomalies), between 2 and 4 cm at DBH and the closest to the center of the quadrat.

1.4.3 Laboratory analysis

Sapling discs were air dried and sanded. Annual growth of the last 25 years was measured to a precision of 0.001 mm under a 40X magnification with an electronic micrometer (Velmex Inc, Bloomfield, N.Y.) coupled with a digital meter (Acurite III,

Jamestown, N.Y.). Annual increment was measured along one radius per disc, located at 30° from the longest radius. Visual examination of the discs was done prior to measurements on at least two additional radii where annual rings were clearly readable to identify partial and false rings.

The soil samples were air dried and sieved (2 mm mesh) prior to analysis. Soil pH was measured with a digital pH meter in a solution of 10 g of soil in 20 ml of 0.01 M $CaCl_2$. The exchangeable cations were extracted with an unbuffered solution of 10 g of soil in 100 ml of 0.1 M $BaCl_2$ + 0.1 M NH_4Cl (Amacher et al., 1990). Cations were measured by inductively coupled plasma emission.

1.4.4 Statistical analysis

The abundance of maple and beech saplings was modelled as a function of environmental characteristics (light and soil properties), taking into account the spatial distribution of adult trees as potential seed sources (Chapter 4). Species abundance per size class was modelled with Redundancy Analysis (RDA), the multivariate extension of multiple regression analysis (Legendre and Legendre, 1998). Size classes were: A) new year seedlings; B) 0-30cm in height; C) 30cm-1m height; D) height > 1 m and DBH < 4cm; E) 4 cm < DBH < 9cm. Abundance data were first square root transformed and then normalized per species/size class to assure equal weights between classes and species. The matrix of explanatory variables comprised base cations availability (Ca, Mg, Na, H+Al, K), pH, PPFD at 1 and 4m, the average radial growth per 5 year period, from 1980 to 2004, and the predicted seed rain (see below for the calculation). Variables describing micro-topography (slope on X and Y axes of the plot, elevation in meters relative to the lowest point of the sub-plot) were also added to the matrix in order to take into account potential impacts of local drainage and reduce the residual errors, although these are not variables of the conceptual model. The radial growth was considered rather than suppression and release history (Chapter 2) because a large fraction of the understory saplings exhibited an exponential increase of growth over time, evidenced by the openness of the overstory canopy. The uniformity of sapling size prevents the impact of size on radial growth. Analysis was conducted in a first step by selecting variables in a forward procedure at the $p = 0.1$ level, and the test of significance of the whole analysis was later performed. Statistical significance was assessed

by comparison of the F statistic to the distribution of the F obtained after 9999 permutations of the abundance matrix.

A common approach to account for the presence of spatial structure in either the modelled or the explanatory variables is to use partial RDA, treating space as a covariable (Borcard et al., 1992). This technique can result however in a large fraction of the variance commonly explained by both the environmental and the spatial variables. This is susceptible to happen when the environmental variables are themselves strongly spatially structured. Moreover, this technique complicates the interpretation of "space" as an explanatory variable, since it does not relate to any biological hypothesis. Indeed, it is common that the fraction of variance explained by the space variables is wrongly interpreted as a quantification of dispersal limitation (e.g. Gilbert and Lechowicz, 2004; see the critique at chapter 4). Dispersal limitation was included in the above model using the predicted seed rain composition following the technique of Ribbens et al. (1994). We do not expect this variable to have a good fit with large saplings because the actual distribution of adult trees is not necessarily representative of the one that gave them birth, but it is necessary to take it into account to model seedling distribution in relation to environmental variables (Chapter 4). The seed rain at each quadrat was thus predicted using the spatial distribution and DBH of each tree > 9.1 cm at DBH from the extended plot. A Weibull dispersal kernel with a theta of two was used, and the mean dispersal distances for sugar maple and beech were respectively 8 and 6 meters based on Ribbens et al. (1994). Results were not however sensitive to the average dispersal distance in the range of 5 to 10 meters. We did not take into account seedbeds since maple and beech are large-seeded species with low substrate limitations (Caspersen and Saprunoff, 2005). The origin of beech seedlings and saplings (seed versus root sprouts) was not determined because sprouts were rare at the site. Residuals of the RDAs were finally analysed with the PCNM method (Borcard and Legendre, 2002) in order to quantify the spatial structure not explained by the environmental variables. PCNM variables were also selected by a forward procedure at $p = 0.1$ level.

1.5 Results

When all the size classes are included in the model, 26.2 % of the variance (adjusted R^2, $p < 0.001$) was explained by 10 variables (Tables 1.1 and 1.2). The ordination is presented

at Figure 1.1. The location of quadrats (points) is well dispersed across the ordination space; there are no apparent groups of quadrats or outliers driving the model. Maple of size classes B-C and D and beech of class B are positively correlated. Their abundance is positively related to light availability at 1m and to the seed rain of beech, while negatively related to soil pH, sapling growth during the 1990-94 interval and maple seed rain. This group of species and size class is orthonormal to a second group composed of beech in size classes A-C and D. Abundance of beech in class A is meaningless since most quadrats had no new year seedlings, presumably because of a low seed crop. The abundance of this group is positively related to elevation, exchangeable acidity and negatively related to growth during the 2000-04 interval and soil pH. The relationship with the predicted seed rain is weak for both species. Finally, stems in the largest size class (E) are related for both species, with their abundance positively related to growth during the 1990-94 period, the seed rain of sugar maple and pH. These species/size class are also negatively related to the group including sugar maple of size classes B-D and beech class B.

Because of the elevated number of variables included in the selection procedure and the low variance explained, it is likely that many correlations are spurious. When plotting the abundance of each size class against the selected environmental variables, for most variables there is no clear pattern emerging (see figure 1.2 for an example with size class C). In some cases, like at figure 1.2D, the relationship could be related to the frequency distribution of the data being skewed. Another example of spurious

Table 1.1 Summary of the Redundancy Analysis.

Size class	Environmental variables				PCNM variables on residuals			
	R2	R2adj.	p	N variables	R2	R2adj.	p	N variables
All	0.349	0.262	<0.001	10	0.217	0.136	<0.001	8
(A) New year seedlings	0.490	0.422	<0.001	10	0.308	0.216	<0.001	10
(B) Height 0 – 30cm	0.443	0.416	<0.001	4	0.241	0.173	<0.001	7
(C) Height 30cm – 100cm	0.327	0.285	<0.001	5	0.341	0.272	<0.001	8
(D) Height > 1 m and DBH < 4.0 cm	0.191	0.151	<0.001	4	0.214	0.164	<0.001	5
(E) 4.0cm <DBH< 9.0 cm	0.203	0.164	<0.001	4	0.642	0.539	<0.001	19

Table 1.2. List of the environmental factors selected by the forward procedure at $p < 0.1$. Variables are sorted by their p values at the entry into the model. Details on variables: Growth: past radial growth for the period starting at year indicated by the variable; Abbreviations are for: Seeds: predicted seed rain; PPFD: Percentage of photon flux density; Exch.: exchangeable cations; B.S.: base cation saturation.

	Size class					
	All	A	B	C	D	E
1	Seeds-SM	Seeds-SM	PPFD-1m	Seeds-SM	Growth-1990	Growth-1990
2	Growth-1990	Growth-2000	Seeds-SM	PPFD-4m	Exch. H+Al	Seeds-SM
3	PPFD-1m	Slope Y	Growth-1990	Elevation	pH	Growth-1985
4	Exch. H+Al	Exch. B.S.	Seeds-AB	Growth-1990	PPFD-1m	PPFD-1m
5	Seeds-AB	PPFD-4m		PPFD-1m		
6	Slope Y	Exch. Na				
7	Growth-2000	Seeds-AB				
8	Exch. Mg	Growth-1995				
9	Elevation	Exch. K				
10	pH	pH				

Figure 1.1 Biplot of the Redundancy Analysis (RDA) of sugar maple and American beech regeneration density after forward selection of the environmental variables at $p < 0.1$. Abundance data were standardized prior to the analysis. The full arrows represent environmental vectors and pointed arrows species positions. The letter following the name of the species indicates the size class.

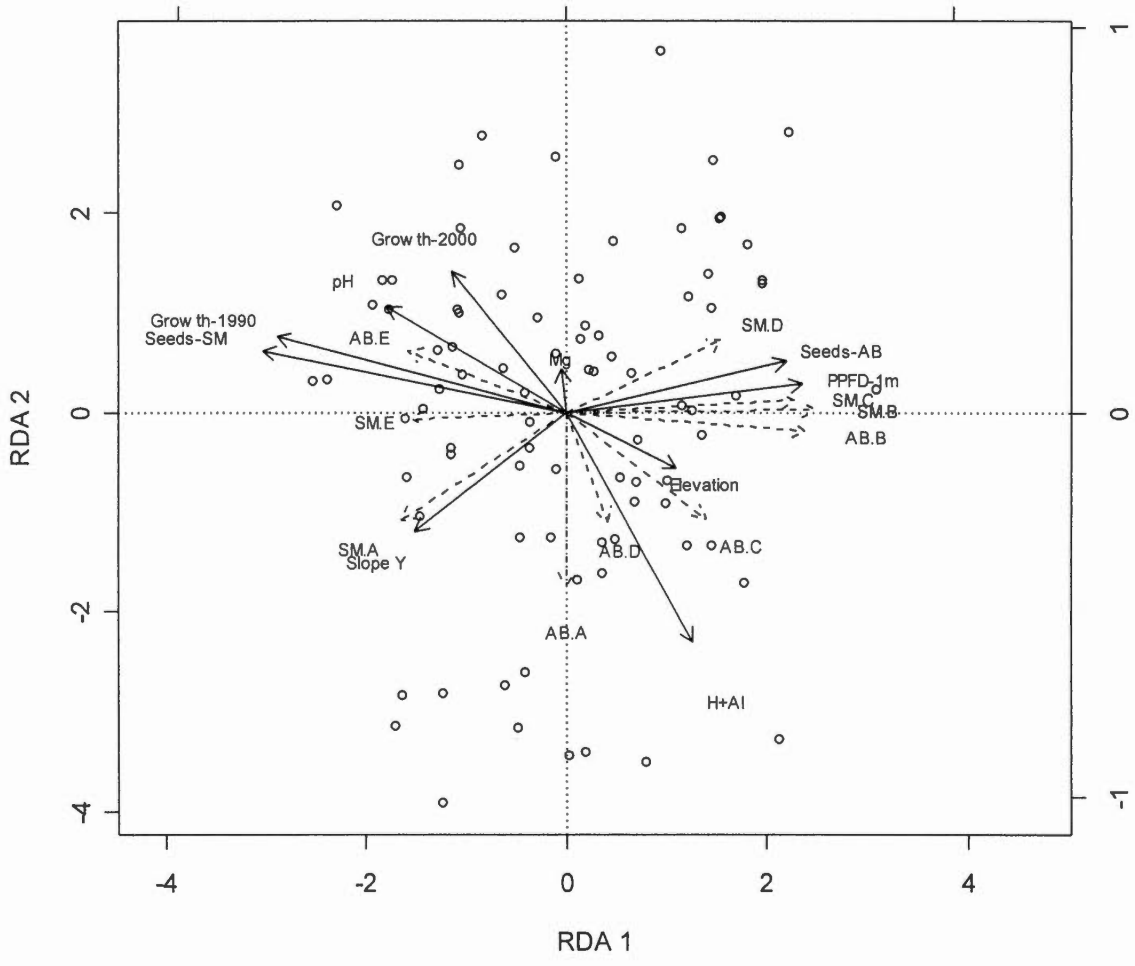


Figure 1.2 Abundance per quadrat for the size class C (30cm to 1m height) as a function of different selected environmental variables. Full circles for sugar maple and open circles for American beech.

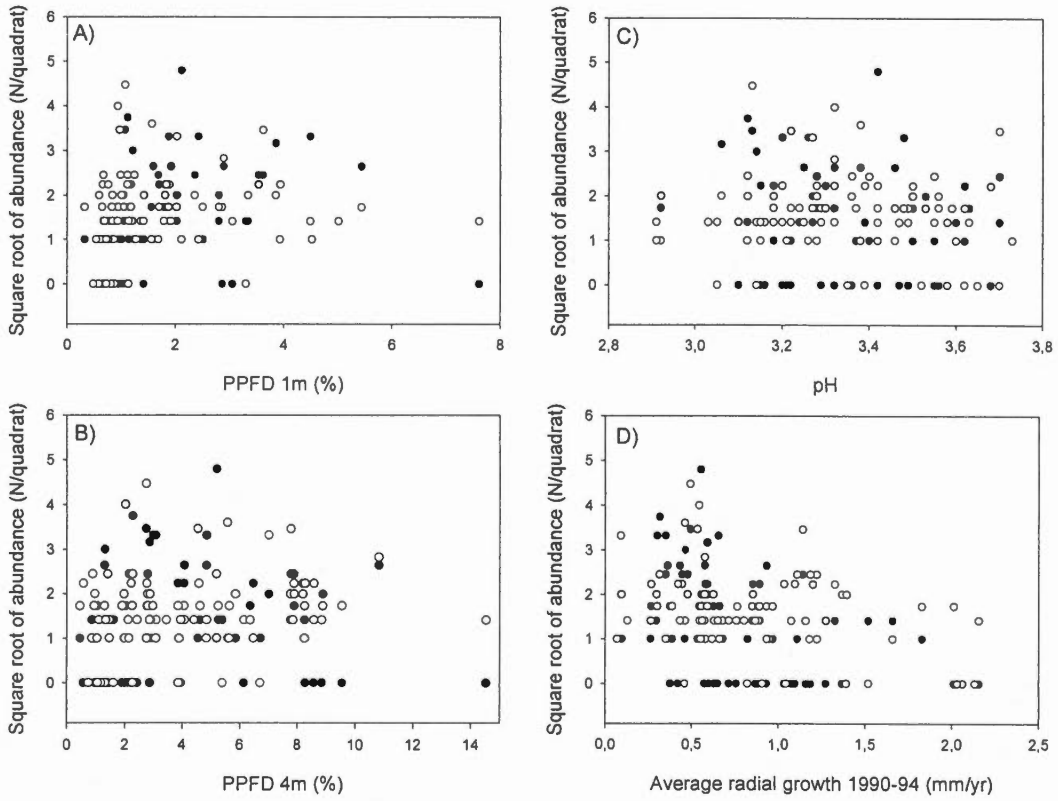
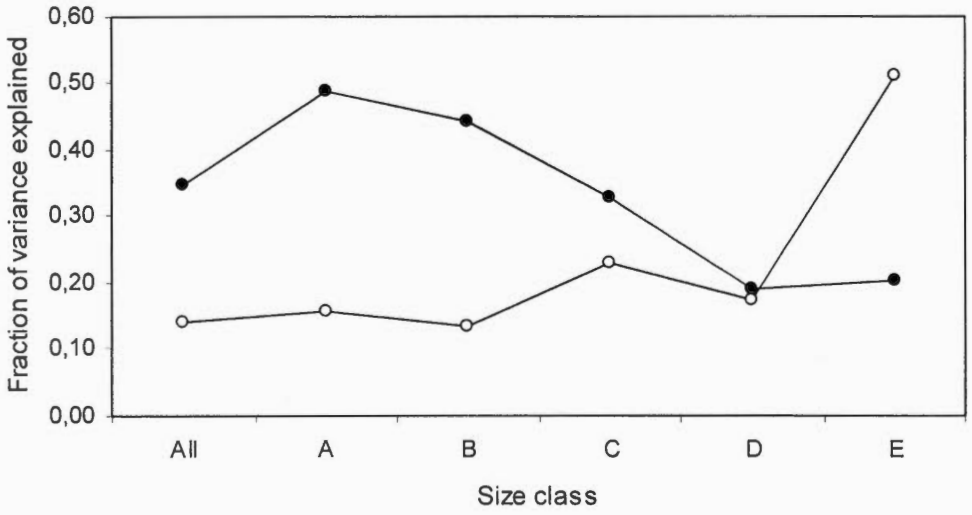


Figure 1.3 Fraction of variance explained by the RDA (R^2 - not adjusted) by size class. The full circles represents analysis of species abundance as a function of the selected environmental factors (see table 1.2 for a list of the variables) and the open circles represent analysis of the residuals of the RDAs with the environmental factor as a function of the selected PCNM variables (selected at $p < 0.1$ – fraction of the variance in the abundance data, not the residuals).



correlations is the selection of previous year's growth on the abundance of newly germinated seedlings (Table 1.2).

The fraction of variance explained by the model decreased with size class (Figure 1.3). There was no relationship between size class and the residual fraction explained by the spatial variables. The residuals for the model of size class E are however highly spatially structured. The fraction of the residuals explained by the PCNM variables is 0.539 (R^2 adj.). The variables selected differed between size classes (Table 1.2). There is however no pattern in the change of selected variables with increasing size.

1.6 Discussion

The first hypothesis tested here is that species composition is related to environmental characteristics. The conceptual model synthesized in the introduction predicts that relative abundance of maple and beech will vary spatially, considering the spatial distribution of parent trees (Chapter 4), with light availability, soil properties and past disturbance history. This test has been conducted previously at the regional (Chapter 2) and the landscape scale (Arii and Lechowicz, 2002), but not at the local scale. Results presented here show the species abundance is somewhat related to the environmental characteristics. The fraction of explained variation in species abundances is however relatively small and a close examination of the data shows that these relationships are weak and might be spurious. The relationship between species abundance and the different variables is in some cases coherent with the model (e.g. beech of classes C-D is positively correlated to exchangeable acidity, maple of classes B-C is positively correlated to light availability at 1m), but in other cases is not (e.g. maple in classes B-D is negatively related to soil pH).

The ordination of species abundance per size class suggests that maple and beech are differentiated in space in the smallest size classes. The abundance of regeneration between 30cm height and 4cm at DBH is orthornormal (no correlation) between maple and beech. The saplings of the larger size classes are however positively related between the species. This result agrees with the regeneration niche hypothesis (Grubb, 1977) where speces coexist on the same environment as adults because of differentiation at the seedling stage, but not the conceptual model. It could reflect some past recruitment cohorts. The opening of the canopy

is usually followed by a massive recruitment (Poulson and Platt, 1996; Beaudet et al., 2007), which will grow and cast much of light, preventing further establishment (Beaudet et al., 2007). The abundance of larger saplings would then be negatively related to the abundance in the smallest classes, especially for maple which has a lower survival in shade. However, the abundance of both species in the largest class is related to the average growth from 1985 to 1994.

We also tested if the variables predicting species distribution will change with size because of increasing environmental filtering. According to the conceptual model of coexistence, we would expect the seed rain, measured light availability and soil fertility to be good predictors of small size class abundance and past growth history and soil fertility to better predict larger saplings abundance. The selected variables do effectively change with size, but not in a coherent manner. The pattern that emerges, in terms of selected variables as a function of size class, rather suggests some variables were selected by chance alone. For instance, the predicted seed rain of maple is selected as one variable to model distribution of the largest size class, while the growth in the 1990-94 interval is selected as the second best predictor of newly germinated seedling abundance. Moreover, the fraction of variance explained by the model decreases with increasing size. Environmental filtering predicts the opposite since dispersal is a stochastic process and selection a deterministic one which effect will increase with time.

Then why doesn't the spatial distribution of maple and beech saplings match the prediction of the conceptual model of coexistence for maple and beech? The first possibility is the quality of the dataset. The examination of the spatial distribution of the different variables studied (appendix) reveals strong spatial patterns in all variables. For instance, 74.7% of the variance of the soil pH was explained by 9 PCNM variables selected in a forward procedure. The occurrence of such patterns immediately rules out the possibility of bad quality sampling and laboratory analysis Such a situation would have resulted in a random distribution of the variables, which is obviously not the case. However, the studied variables might be inadequate. For instance, soil was sampled at the B horizon. Studies relating soil properties to maple and beech abundance did sample at fixed depths or in the humus layer (Finzi et al., 1998; Woods, 2000; Arii and Lechowicz, 2002). Past growth

history could also be an inadequate approximation of past light conditions, or not a limiting factor in the recent years. Radial growth did increase steadily from 0.49 mm/yr on average in the 1980-84 interval to 0.98 mm/yr for the 2000-04 interval. An ontogenic change of radial growth could explain part of this change, but is not that strong for saplings of this size (Chapter 2). Finally, the presence of spatial structure in the residuals (Table 1.1) suggests there are underlying patterns that haven't been taken into account into the model. However, this fraction of variance is relatively small.

This questioning about the quality of the dataset however remembers past criticisms devoted to the competitive exclusion principle and the niche theory (Hardin, 1960). If one observes coexistence but not niche differentiation, is it because the competitive exclusion principle is wrong or because we did not measured the right variables? This reasoning has been criticized because of its strong circularity (Hardin, 1960). There are indeed some results presented here that are strongly supported by the data and goes against the conceptual model of coexistence for maple and beech. Even if the characterisation of the environment would have been wrong because of inadequate sampling or environmental variables, the species/size class ordination clearly goes against the conceptual model. Moreover, to assess if sampling intensity was sufficient, a principal components analysis was conducted on the abundance data for a larger plot of 100 X 50 meters (200 quadrats) and results were exactly the same. Small classes were still orthonormal and the largest class strongly correlated between species. At the very least, species/size class ordination is adequate because it is not affected by the quality of the environmental data and the sampling intensity.

The most interesting result of this study is perhaps the decreasing fraction of variance explained by the model with the increase in sapling size. This pattern could result from having the wrong explanatory variables for the larger size classes (e.g. a change in time in soil properties or in seed rain distribution), or with the accumulation in stochastic events affecting sapling distribution. The fraction of the unexplained variance in the functional relationships at the basis of the conceptual model is usually high. For instance, for the relationship between light availability and sapling growth, Kobe (1996) reported regression coefficients ranging from 0.17 to 0.79, while Bigelow and Canham (2002) reported coefficients around 0.25 (even with the inclusion of soil fertility as a second explanatory

variable). High variability in life history traits differentiating species, even if species are statistically different, can result in almost unpredictable dynamics (Chapter 5). The resulting dynamics can either be neutral or extremely stable, but in both cases the relationship between species distribution and the environment will be low. Even if the average dynamics across an elevated number of samples can satisfies predictions from life history traits, the variance will be too elevated to adequately predict the dynamics for a single sample (Chapter 5).

The results presented in this study do not agree with the predictions of the conceptual model of coexistence for maple and beech. An alternative hypothesis to their coexistence could be a competition/colonization trade-off for maple and beech. Here, we tested whether the spatial distribution could be explained partly by dispersal limitations. If beech had been more dispersal limited than maple, then beech seedlings' spatial distribution would have been better predicted by the spatial distribution of the parents than maple. Although the predicted seed rain was selected to model the distribution of both species, the ordination shows these relations can be spurious. Perhaps, the abundance of adult trees was sufficiently elevated to prevent dispersal limitations for both species, which would have limited our analysis. In this situation however, dispersal limitation could not act as a coexistence mechanism.

In face of these failures to explain maple and beech coexistence, it is legitimate to ask if there is stable coexistence between maple and beech at the local scale. Recent theoretical advances on neutral dynamics (Hubbell, 2001), dynamics at the limiting similarity (Chapter 3, Schaeffer and van Ness, 2006) and coexistence mechanisms among forest trees (Chapter 6), demonstrate that competitive exclusion among forest trees could be extremely slow, especially among species that are highly similar and subject to elevated demographic stochasticity. Coexistence at the local scale could be transient (Holt, 2006). For instance, starting from Forcier (1975), if maple does have a superior establishment early in succession (better colonist) and beech is a superior competitor, but if the time for competitive exclusion to occur is largely superior to the one between intermediate or major disturbances, then at the local community scale, even for old-growth stands, coexistence will be mostly transient. This is basically the same model as the one tested in this study, related to the same coexistence mechanisms, but rather than predicting forever coexistence within a group of few individuals

in the absence of major disturbance, it predicts coexistence for a much larger community in space and with a wider range of disturbances.

This example illustrates the idea that the conceptual model of coexistence for maple and beech could be right, but at larger spatial and temporal scales. The range of environmental conditions necessary for maple and beech differentiation based on their functional responses to the environment might be too wide in relation to the range of conditions encountered in a mature community with only small-scale disturbances. At the site we studied here, on the extended plot of 0.5 ha where light measurements have been measured (200 quadrats), light availability at 1m height varied between 0.3 and 16.9%, but the average was only 1.9% and 75% of the sites were below 2.1%. If for species to differentiate sites with more than 5% must be common, then the actual range of light conditions is far to narrow to allow stable coexistence within the plot. Coexistence would be stable when the range of environmental conditions is large, but almost neutral when conditions are restricted to a narrow range of conditions along the gradient (Chapter 3). If the environmental variability encountered within a local community is small relative to the gradient necessary for their stable coexistence, coexistence will be stable only at the regional scale, the dynamics will be neutral at some localities and competitive exclusion will occur at others (Chapter 3; Mouquet and Loreau, 2002).

1.7 Conclusion

The results presented in this study showed that environmental characteristics are not good predictors of within-stand small scale variation in sugar maple and beech sapling abundance. This suggests that the conceptual model of coexistence for sugar maple and beech might not be adequate for predicting dynamics at this scale. We proposed that this could result from a dynamics dominated by demographic stochasticity or be due to transient dynamics. In any case, dynamics are rather unstable. Any historical factor affecting preferentially one species or the other, such as a past logging episode or a wind storm, will considerably impact the species relative abundance. The composition of the community following the disturbance is expected to have more profound effects on species relative abundance than the environmental conditions. For the forest manager interested in the relative abundance of these two species, this perspective has important implications. Because

environmental differentiation is weak, this suggests that a direct manipulation of species abundance, for instance by plantation or a selected removal of saplings, will have much more implications on future species relative abundance than a manipulation of the environment such as logging or fertilization.

1.8 Appendix

Figure 1.1A Spatial distribution of the regeneration density (in stems/quadrat) of sugar maple (left) and American beech (right). A-B) 1yr-old seedlings; C-D) 0-30cm height seedlings; E-F) 30-100cm height seedlings; G-H) 100cm height – 4.0 cm at DBH saplings; I-J) 4.1 – 9.0 cm at DBH saplings.

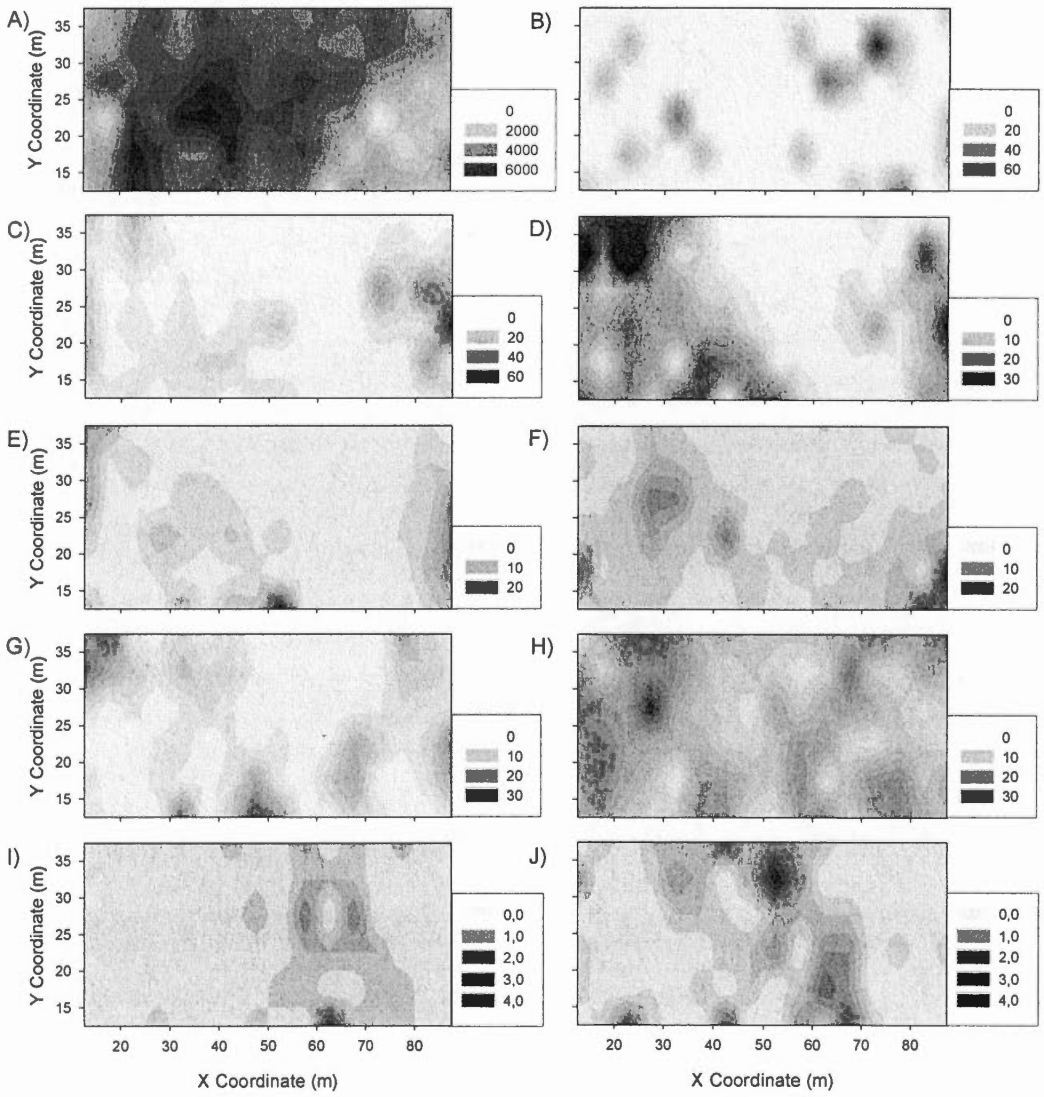


Figure 1.2A Spatial distribution of basal area (m^2/quadrat) of trees with DBH > 9 cm. A) Sugar maple; B) American beech; C) All species.

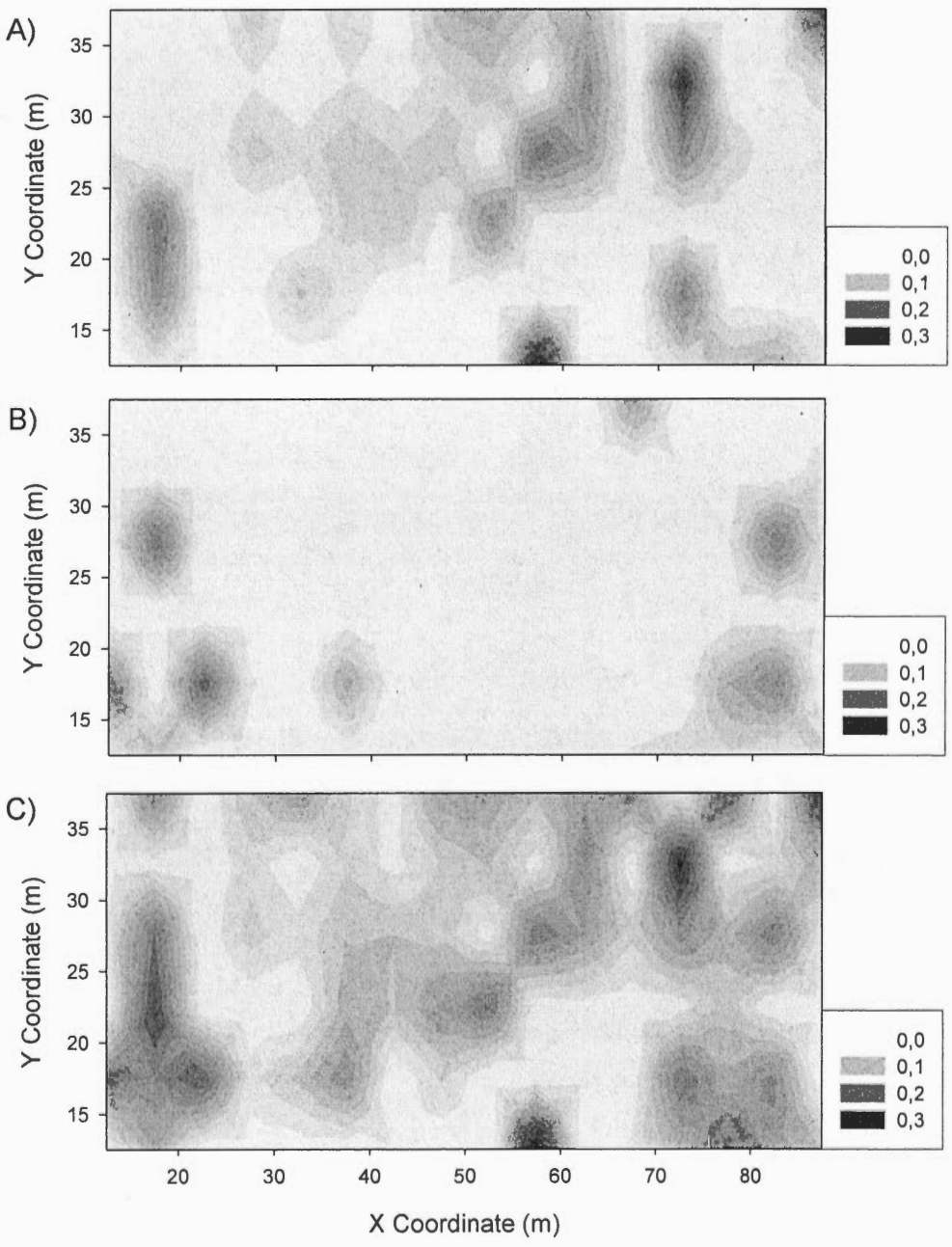


Figure 1.3A Spatial distribution of light availability in %PPFD at A) 1m and B) 4m height.

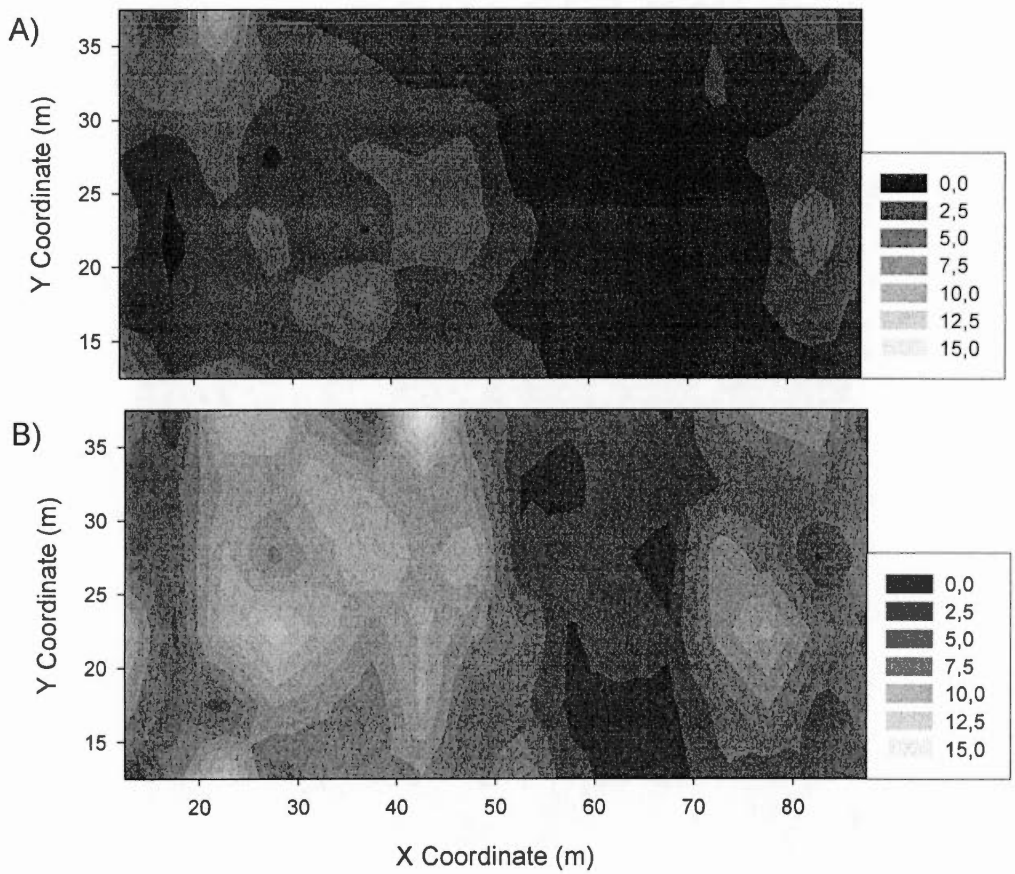


Figure 1.4A Spatial distribution of soil properties. A) pH; B) Exchangeable acidity (cmol+/kg); C) Base cation saturation; D) Exchangeable cations (cmol+/kg); E) Exchangeable magnesium (cmol+/kg).

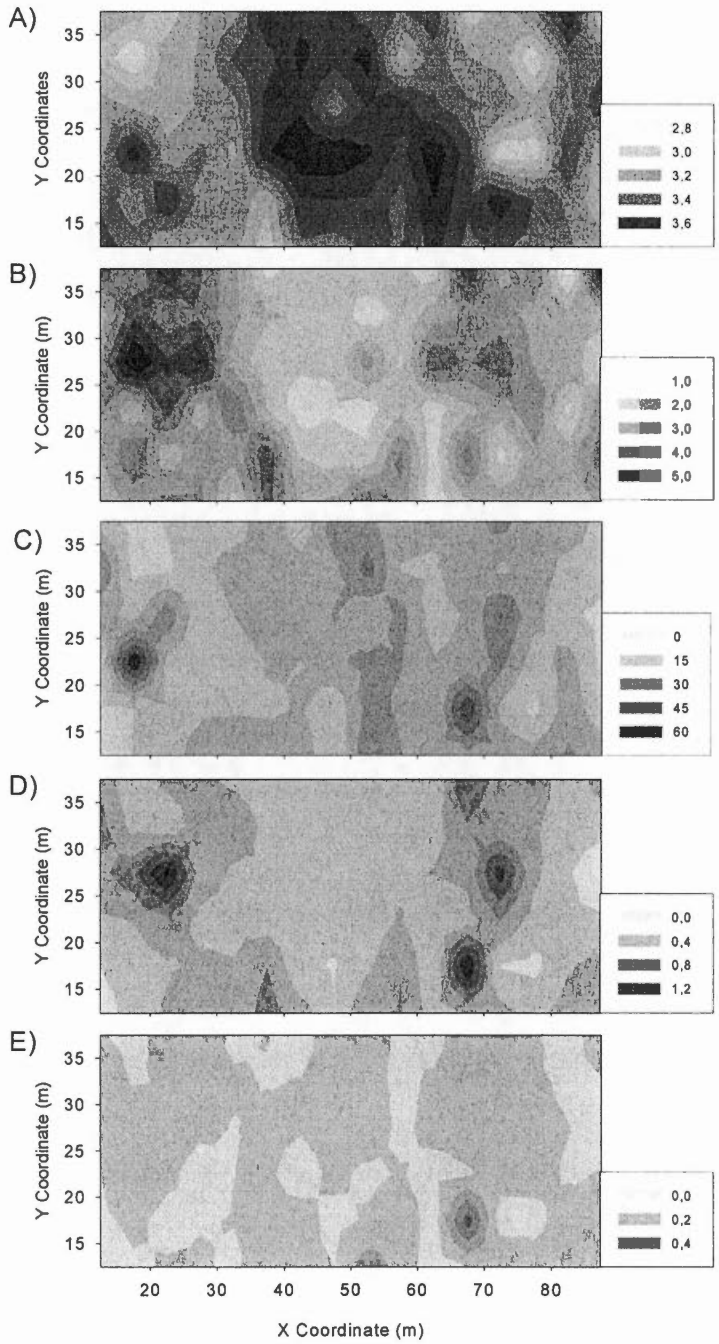
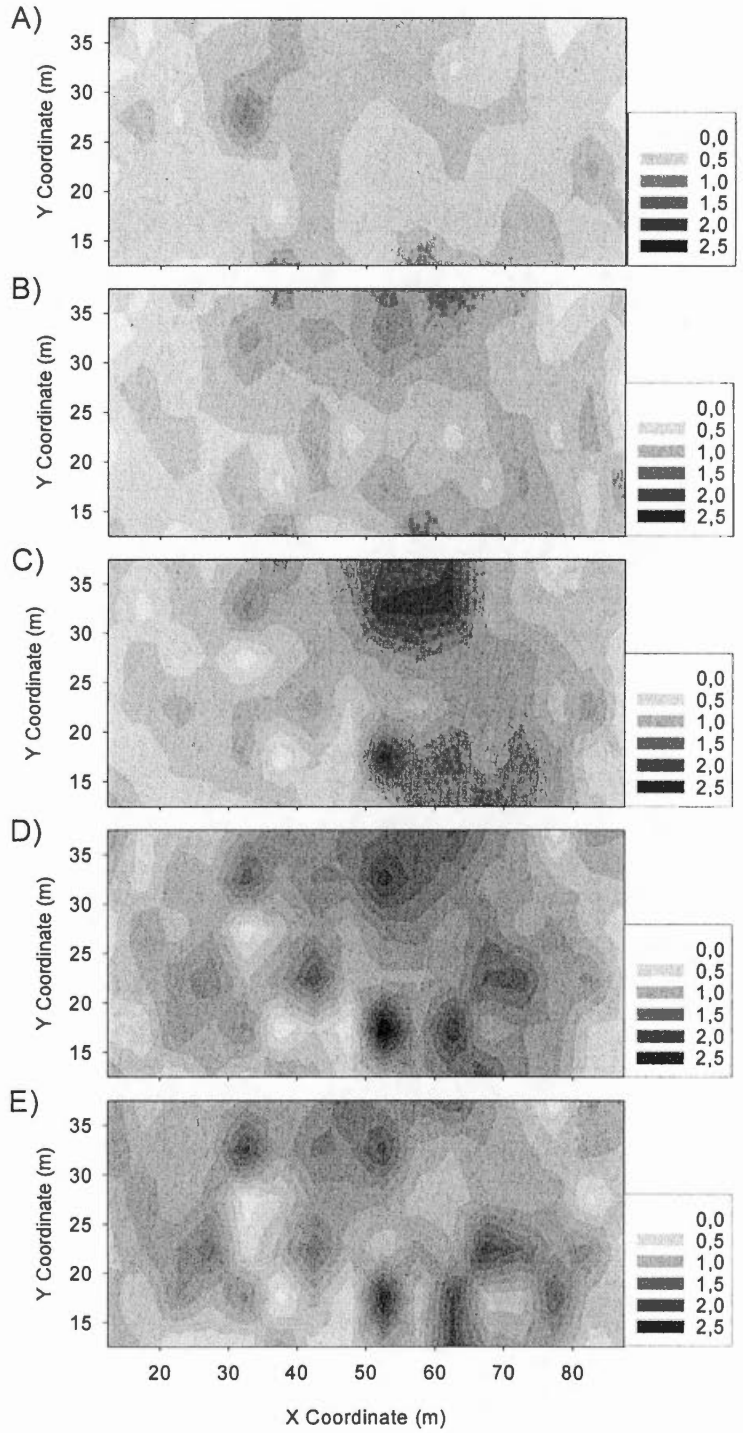


Figure 1.5A Spatial distribution of average growth (in mm/year) of understory saplings per 5 year-intervals. A) 1980-84; B) 1985-89; C) 1990-1994; D) 1995-1999; E) 2000-2004.



CHAPITRE II

CHANGES IN SAPLING RECRUITMENT DYNAMICS OF *ACER SACCHARUM* AND *FAGUS GRANDIFOLIA* OVER 40 YEARS IN DECIDUOUS FORESTS OF SOUTHERN QUEBEC

Dominique Gravel, Marilou Beaudet, Christian Messier

2.1 Résumé

La composition et la dynamique de communautés forestières matures n'est pas stable à l'échelle locale en raison de nombreux processus comme les perturbations. Néanmoins, il n'est pas évident si des processus peuvent synchroniser la dynamique à l'échelle régionale. Les forêts d'érable à sucre et de hêtre à grandes feuilles du sud du Québec constituent un bon exemple de communautés qui sont actuellement sujette à un changement de la dynamique de régénération à l'échelle régionale. Les objectifs de cette étude étaient d'abord de décrire la dynamique de recrutement qui a conduit à l'augmentation récente du hêtre parmi la régénération, et ensuite de tester trois causes potentielles au patron observé. Une analyse dendrochronologique de la croissance des gaulis et de leur structure d'âge a été conduite au sein de 34 peuplements du sud du Québec pour tester si le changement de recrutement serait associé au lessivage des cations basiques du sol, à un épisode de dépérissement survenu dans la décennie 1980 ou un changement progressif de l'environnement du sous-étage causé par la succession. La comparaison des structures d'âge a révélé un échec de la régénération de l'érable à sucre par rapport au hêtre qui a commencé il y a environ 40 ans. L'augmentation du hêtre est progressive et le dépérissement n'a pas eu d'effet sur la structure d'âge. L'analyse des patrons de croissance au fil du temps a révélé un changement majeur de la hiérarchie entre les deux espèces depuis les années 1980, en faveur du hêtre. Le déclin relatif de la croissance de l'érable à sucre n'est cependant pas associé à la fertilité du sol, suggérant que le lessivage des cations basiques ne serait pas impliqué dans ce changement. L'historique de suppression et de libérations des gaulis explique la majeure partie de la variation de la croissance. Pour les deux espèces on trouve un patron en U de la proportion de tiges en libération au travers des 40 dernières années, avec la décennie 1980 au creux de ce patron. L'historique de suppression et de libération est également le facteur qui explique la plus grande proportion de la variance de la composition entre les sites. Cette étude démontre que la dynamique de recrutement d'espèces tolérantes à l'ombre peut être partiellement synchronisée à l'échelle régionale. Des études futures sur la dynamique des trouées devraient être conduites pour identifier les processus responsables d'une telle synchronisation régionale.

Mots clés : Érable à sucre, hêtre à grandes feuilles, dynamique des gaulis, recrutement, lessivage des cations basiques, dépérissement, trouées, libération de croissance

2.2 Abstract

The composition and dynamics of mature forest communities is not stable at the local scale because of numerous processes such as disturbances. However, it is less clear if there are any processes that could synchronize forest community dynamics at the regional scale. Sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) forests in southern Quebec provide a good example of communities that are globally facing a change in sapling recruitment dynamics at such a regional scale. The objectives of this study were firstly to describe the recruitment dynamics leading to the recent increase in beech among saplings, and secondly to investigate three potential causes for the observed pattern. A dendrochronological analysis of sapling growth and age structure across 34 stands in southern Quebec was performed to test if the change in recruitment was related to base cation leaching, a decline episode in the 1980's or a progressive change in the understory environment caused by succession. The comparison of sapling age structure revealed a recruitment failure of maple relative to beech that started about 40 years ago. The increase in beech was progressive and the decline episode did not impact the age structure. The analysis of the growth pattern over time revealed a change in hierarchy since the 1980's in favour of beech. Maple growth decline was not related to the soil fertility, suggesting that base cation leaching is not responsible for this change. The suppression and release history explained much of the variance in growth for both species. Both species exhibited a U-shaped pattern in the proportion of stems in release over the last 40 yrs, with the lowest rates of release corresponding to the 1980's. The suppression and release history was the factor explaining the greatest proportion of the variance among sites in sapling abundance. This study showed that sapling recruitment dynamics of shade tolerant species can be partially synchronized at the regional scale, despite potential variation among stands at a more local scale. Further studies on gap dynamics should aim at identifying processes responsible for such synchronicity across regions.

2.3 Introduction

Large scale synchronous variations in forest tree species composition are not common nor well documented (Clark and McLachlan, 2003; Liebhold et al., 2004; Laurance et al., 2004). We know from other ecosystems there are three different mechanisms responsible for spatially synchronized fluctuations in population densities: i) dispersal of individuals from a source population, ii) populations' dependence on an exogenous factor that is spatially synchronized (the Moran effect), and iii) trophic interactions with other organisms that are spatially synchronized (Liebhold et al., 2004). In the case of forest trees, with a relatively limited dispersal, the most likely mechanism is the second one, i.e. the response to an exogenous factor, although some forest communities are also affected by interactions with other organisms, such as insects and pathogens.

Sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.), two highly shade tolerant tree species dominating the deciduous forests in North America, is a great system to improve our knowledge on this phenomenon. Short- and long-term changes in their relative abundance have been reported in the literature, in both managed and old-growth forests, some in favour of maple (e.g. Abrell and Jackson, 1977; Siccama, 1971, McIntosh, 1972, Runkle, 1990; Fain et al. 1994; Poulson and Platt, 1996; Foré et al., 1997), others in favour of beech (e.g. Brisson et al., 1994; Woods, 2000; Forrester and Runkle, 2000; Duchesne et al., 2005; Angers et al., 2005). It is recognized that the species composition in mature forests dominated by shade tolerant species such as these does not reach a stable state, even in old-growth forests, but rather follows natural fluctuations (see the conceptual models in Poulson and Platt, 1996, and Woods, 2000).

There have been numerous reports over the last decades of an unexpected increase in the abundance of beech saplings relative to maple in various regions of the species range (Ostrowsky and McCormack, 1986; Jenkins, 1997; Ray et al., 1999; Schwarcz et al., 2001; Forrester et al., 2003; Hane, 2003; Duchesne et al. 2005; Angers et al., 2005). For instance, at Hubbard Brook, the density of beech saplings (< 10 cm DBH) increased five-fold from 1967 to 1997, while maple seedlings (< 50 cm tall) declined twenty-fold and small saplings (2-5 cm DBH) declined by 80% (Hane, 2003). A recruitment failure of sugar maple was reported by Jenkins (1997) in the Adirondacks. In southern Quebec, near the northeastern limit of the

species range, Duchesne et al. (2005) reported a 17% decline in maple density among stems < 29.25 cm DBH over the last 10 years, and beech saplings density has nearly doubled. Beech sapling density almost doubled from the 1980's to 1990's in Quebec's forest inventory data, while maple slightly decreased during the same period (Annexe). An elevated abundance of beech among saplings has been reported in both managed and old-growth forests (Brisson et al., 1994; Schwarcz et al., 2001; Angers et al., 2005).

The coexistence and patterns of variation in the relative abundance of maple and beech are hypothesized to result from subtle interspecific differences in shade tolerance and response to soil fertility (Canham, 1989; 1990; Poulson and Platt, 1996; Beaudet et al., 1999; Woods, 2000; Arii and Lechowicz, 2002). Maple is usually expected to increase in abundance with an increase in the frequency of small scale disturbances because it benefits more from an opening of the canopy due to faster growth, than beech under higher light (Canham, 1989). Beech, on the other hand, is expected to increase in dominance when the disturbance rate is low, due to higher survival and growth in dark understories (Canham, 1989; Kobe et al., 1995). Soil fertility presumably impacts the spatial distribution of these species (van Breemen et al., 1997; Arii and Lechowicz, 2002), since growth and survival of maple is also positively affected by base cation availability (Kobe, 1996; Kobe et al., 2002). Exogenous factors (e.g. climate change, atmospheric deposition and logging) could impact both the disturbance regime and soil properties at different spatial and temporal scales and thus regulate the relative abundance of the species (Poulson and Platt, 1996).

The first objective of this study was to describe the dynamics of recruitment responsible for the recent increase in the absolute density and relative abundance of beech saplings in the understory of mature maple – beech communities over there range in southern Quebec, Canada. The second objective was to investigate the possible causes of the observed pattern. Three hypotheses were considered. First, base cation leaching by acidic depositions could have stressed maple regeneration, as proposed by Jenkins (1997), Kobe et al. (2002), and Lovett and Mitchell (2004). Secondly, crown thinning during the 1980's episode of maple decline (Bernier et al., 1989; Houle, 1990) might have benefited beech saplings more than maple (as proposed by Duchesne et al., 2005 – note that we distinguished between base cation leaching and decline episode, we do not assume these are necessarily linked). Finally,

a progressive decrease in understory light availability associated with forest succession might have occurred and would favour beech over maple (as proposed by Poulson and Platt, 1996 and Beaudet et al., 1999). Note that these hypotheses are not necessarily mutually exclusive.

We investigated these possible causes by analyzing sapling age structure, radial growth chronologies, suppression and release histories and demographic records of 34 mature maple-beech stands from a wide range of soil conditions in Quebec. Half of these stands were considered healthy and half declined during the 1980's maple decline episode. According to the first hypothesis, we would expect to observe a recent recruitment failure of maple relative to beech in the sapling age structure, a decline in radial growth of maple related to soil characteristics (i.e., present only, or more pronounced on soils more susceptible to base cation leaching), and a positive correlation between maple relative abundance among saplings and soil fertility. If the second hypothesis was true, we would expect to observe a peak in the recruitment of beech in declining stands, a distinct pattern in the suppression and release history between healthy and declined stands, and a higher relative abundance of beech saplings in declined vs. healthy stands. Finally, under the third hypothesis, we would expect a progressive decrease over time in the proportion of stems under suppression, and that differences in both species sapling relative abundance among stands would be correlated to the suppression and release history.

2.4 Methodology

2.4.1 Study area and sites

Sampling was conducted in the Eastern Townships and Portneuf regions in southern Quebec. These regions are respectively located in the sugar maple – yellow birch (*Betula alleghaniensis* Britton), and in the sugar maple – American basswood (*Tilia americana* L.) bioclimatic domains (Robitaille and Saucier, 1998). Sampling was conducted in 20 and 14 stands in the Eastern Townships and Portneuf regions respectively. The overstory of the sampled stands was composed of a mixture of tree species including sugar maple, beech, *Betula alleghaniensis* Britton, *Acer rubrum* L., *Ostrya virgiana* (Mill.) Koch, *Fraxinus Americana* L., *Tsuga canadensis* (L.) Carr., *Abies balsamea* (L.) Mill. and *Picea rubens Sarg.* Mean annual temperature ranges from 2.5 to 5.0°C, the length of the growing season varies

from 170 to 190 days, and mean annual precipitation varies from 1 000 to 1 200 mm (Robitaille and Saucier, 1998). Glacial till is the dominant deposit in the two regions. The dominant soil type for the stands sampled in the two regions is the eluviated dystric brunisol, and the humus type is usually a moder.

We pre-selected potential stands by overlapping a stand map elaborated by professional photo-interpreters with a map of the levels of maple decline established by aerial surveys in 1985-1986 by Bordeleau (1987). Potential stands were classified as healthy (0% to 10% of canopy coloration and thinning) or lightly to moderately declining (11% to 50% of canopy coloration and thinning). Potential stands were visited in 2003 and only stands which met the following criteria were kept for study: basal area (BA) > 20 m^2/ha, presence of trees > 30 cm in DBH and relative BA of beech (among trees > 9 cm in DBH) was > 5%; Sampling was restricted to stands with no signs of recent disturbances, such as heavy damage by the 1998 ice storm or presence logging stumps. A total of 34 stands were kept for further study (Table 2.1).

2.4.2 Field sampling

Sampling in each of the 34 stands was performed at three locations, > 100 m apart along a transect. The starting location of the transect and of the first plot was determined randomly on the stand map prior to sampling. At each of the three sampling locations, the stems (DBH > 9 cm) of all species were recorded in a 400 m^2 plot (11.28 m radius). Saplings (height > 1.3 m to 9.0 cm at DBH) were measured in a 100 m^2 subplot (5.64 m radius). At each transect, 10 maple and 10 beech saplings (1.1 - 9.0 cm at DBH) were randomly selected among the three plots and a disc was harvested for each at 20 cm above-ground. Additional larger saplings (DBH from 5.1 to 9.0 cm) were harvested (in some cases outside the plots but along the transect) to complete the sample to a minimum of 5 individuals per species in the 5.1 to 9.0 cm DBH class to ensure a minimal representation of larger saplings for growth analysis. However, the latter saplings were not included into the age structure analysis. Two soil samples per plot were collected, each at 3 to 5 m on opposite sides from the plot center, at 5-15 cm below the top of the B horizon.

Table 2.1 Summary information (mean ± 1SE) about the 34 study sites grouped into a declining and healthy class.

Decline status in the 1980's	Declining		Healthy	
Nb stands	17		17	
Saplings[¥] density (stems/ha)				
All species	3488	± 347	3865	± 3312
Sugar maple	681	± 173	574	± 145
Beech	1866	± 290	1929	± 267
Overstory[§] basal area (m^2/ha)				
All species	27.9	± 1.0	31.8	± 1.3
Sugar maple	16.3	± 1.6	18.3	± 2.0
Beech	6.3	± 1.2	7.9	± 1.1
Soil Properties				
Exchangeable acidity (cmol+/kg)	2.9468	± 0.2477	2.9995	± 0.1769
Potassium (cmol+/kg)	0.0898	± 0.0107	0.0852	± 0.0086
Calcium (cmol+/kg)	0.4706	± 0.0760	0.5555	± 0.1157
Magnesium (cmol+/kg)	0.0795	± 0.0096	0.0713	± 0.0076
Cation exchange capaticy (cmol+/kg)	3.6860	± 0.2901	3.8040	± 0.2093
Base cation saturation (%)	20.12	± 1.71	20.71	± 2.26
pH	4.00	± 0.03	4.01	± 0.02
Sand fraction (%)	53.59	± 2.45	49.46	± 2.63
Loam (%)	37.96	± 2.00	40.90	± 1.61
Clay (%)	8.44	± 0.91	9.64	± 1.31

[¥] Height > 1.3m and DBH < 9 cm

[§] DBH > 9 cm

2.4.3 Laboratory analysis

Sapling discs were air dried and sanded. Annual growth was measured to a precision of 0.001 mm under a 40X magnification with an electronic micrometer (Velmex Inc, Bloomfield, N.Y.) coupled with a digital meter (Acurite III, Jamestown, N.Y.). Measurements were performed along one radius per disc, located at 30° from the longest radius. Visual examination of the discs was done prior to measurement on at least two additional radii where annual rings were clearly readable to identify partial and false rings. Growth increment of partial rings was set at 0 mm. Partial and missing rings are common for maple and beech (Canham, 1990; Lorimer et al., 1999). The series were not cross-dated because i) the series were usually too short (median number of annual rings = 37); ii) there were no apparent wood anomalies that could serve as diagnostic rings for the skeleton plot method (Yamaguchi, 1991); and iii) understory saplings of the studied species generally undergo strong suppression and release episodes (Canham, 1990) that mask the climatic signals and therefore may lead to imprecision in cross-dating series (Lorimer et al., 1999). The series were not standardized to preserve the long term growth trends that constitute an information central to this study. Overall, we recorded the age (at 20 cm height) of 337 maple and 338 beech saplings (5 stems were excluded because of unreadable heartwood). For the subsequent growth series analyses (see below), we focused on the most recent 41 years (1963-2003) in order to have a minimal representation of 3 stems per species/site (there were on average 7 growth series per species/site with > 41 years of growth). The growth series analysis was therefore performed on a total of 251 maple and 230 beech saplings.

The soil samples were air dried and sieved (2 mm mesh) prior to analysis. Analyses were conducted on the composite (based on dry weight) of the six samples taken at each site. Soil pH was measured with a digital pH meter in a solution of 10 g of soil in 20 ml of 0.01 M $CaCl_2$. The exchangeable cations were extracted with an unbuffered solution of 10 g of soil in 100 ml of 0.1 M $BaCl_2$ + 0.1 M NH_4Cl (Amacher et al., 1990). Cations were measured by inductively coupled plasma emission. Texture was measured following the hydrometer method (Gee and Bauder, 1986).2.4.4 Data analysis

2.4.4.1 Comparison of age structure

The frequency distribution of sapling age was compared between species (S) and decline (D) levels using a multiway contingency table, where region (R) was considered as a block (random effect) (Legendre and Legendre, 1998). Age (A) was considered as a categorical variable, using eight 10-year classes (from 20 to 100 years). The Wilks' Chi-square (χ^2_w) statistics was calculated to test for statistical significance after fitting a log linear model. The significance of various terms (mainly interactions between Age and other descriptors) was then evaluated by hierarchically removing terms from the model in a backward selection procedure and testing the significance of the difference of χ^2_w between two successive models using a Likelihood Ratio Test (Legendre and Legendre, 1998). We found no sensitivity to potential site-specific age structures (outliers) after re-analysing the data using a jackknife procedure (10 000 permutations, removing 2 and 4 sites).

2.4.4.2 Identification of periods of release

Individual growth series of suppressed saplings of maple and beech contain, among other valuable information on growth history, both the long-term growth trend and the suppression and release history. Both are of central interest to this study. Numerous methods have been developed to identify sudden growth releases, such as the fixed criteria, the use of a running mean and variants of a standardization procedure (see the review by Rubino and McCarthy, 2004 and references therein). All of these could potentially bias the evaluation of the growth trend in the presence of release episodes either at the beginning or the end of the series. In order to select the best method for our analysis, we compared the fit to the data of five different methods of identification of release episodes with the objective Akaike Information Criterion (AIC) to discriminate among models (details in the Appendix). Twenty-five radial growth series of 41 years were randomly selected, with no distinction between species, region and decline level. The method we developed to identify release events (details in the Appendix) was compared to four traditional methods: the fixed criteria method (release events correspond to departures over a threshold value); the standardization method (departures to the mean of the series); its variant involving a linear detrending (departures to the linear trend); and the moving average method (detection of sudden increase of growth). The iterative method we developed performed the best on the sub-sampled series according to the AIC criteria (Table 2A.1) and therefore identification of release events was

performed on the 481 growth series using this method. Minor and major release episodes were respectively defined as an increase of 100% and 200% in radial growth sustained for a minimum of 4 years (Canham, 1990; Payette et al., 1990).

2.4.4.3 Analysis of growth series

We compared the 41-year-long sapling growth series for difference between species and decline levels for each five year interval (except for the 6-year period of 1998-2003). Comparisons were made with ANOVA, using a split plot design where the sites were included as random effects ("plots"), decline (D) was a fixed between-plot effect, and species (S) a fixed within-plot effect. The regions (R) were also included in the model as blocks. In many cases the residuals were not normally distributed even after transformations of the data. Thus, the value of the F statistic was compared to a distribution of the F statistic after 10 000 permutations of growth for the decision on statistical significance (Legendre and Legendre, 1998). A Bonferonni correction was applied to the P-value to account for multiple testing across a time series (e.g. for $\alpha = 0.5$ and eight time periods, $\alpha_{corr} = 0.5/8 = 0.00625$).

We also compared the early growth series (first 30 years) of young saplings ($\leq$ 30 years old) to early growth series of old saplings ($\geq$ 50 years), within each species every five year interval. The rationale behind this test is that mortality under periods of suppression will select for individuals with higher growth (Landis and Peart, 2005). Thus, young saplings having experienced selection for a shorter period of time should have a slower growth than older saplings, given the same environmental conditions. The null hypothesis (i.-e, constant light environment) is that older saplings are having greater growth. However, early growth would also decreases because base cation leaching also predicts a greater growth of older saplings. Therefore, observing more or equal growth of younger saplings (alternate hypothesis) suggests that the average light conditions were not constant and that the presumed effect of base cation leaching, if any, was not sufficient to counter the effects of a changing light environment. Comparisons among series within species were again conducted by ANOVA at five-year intervals since establishment in a split-plot design, where sites was a random effect and sapling category (young versus old) a within-plot effect. We did not

consider the decline status and the region. Because of stem selection criteria, the sample size for saplings ≤ 30 years old decrease slightly in the age classes of 25 and 30 years old.

We tested for the presence of a growth trend by fitting for each species a model having the year, release status, stem radius and soil base cation saturation as explanatory variables. The full model is:

$$\text{Radial growth} = (GAP+1)*[LLMG*(1 + \beta BS + \gamma \text{Radius}^{\delta}) + (\alpha BS+ \theta)*\text{Year}^{\delta}]$$

where LLMG is the low light minimum growth (theoretical growth when base saturation [BS] and sapling radius are 0 and at the first year of the series). GAP is a variable describing the release status (0 = suppression, 1 = minor release, 2 = major release). The intercept of the trend is a linear function of soil base cations saturation (BS - parameter θ). The trend is a non linear function of stem size (radius) and time (year). The parameter γ scales the relationship with size and δ allows it to be linear or exponential. The parameter α scales the amount of change in growth from year to year. Parameter δ determines the shape of the trend over time (linear, exponential or asymptotic). Parameter β determines the slope of the growth trend as a function of BS. Thus, the trend could be positive on rich sites, while it could be negative on poor sites.

The full model was first evaluated and compared with the AIC to simpler models to test various hypotheses regarding the different factors included in the full model. Model comparison based on differences in AIC assumes independence between observations. Although the growth and gap status are evaluated at the stem level, the sampling unit is the site because soil properties where measured for each site. Thus, the log-likelihood of each observation has been weighted by the inverse of the number of stems at its corresponding site. It allows us to compare models considering all the information contained in the dataset, rather than performing analysis on averaged growth for each site/year.

2.4.4.4 Suppression and release time series

We calculated various descriptors of the suppression and release history of saplings per site and species for the 41-year period mentioned earlier (number of release episodes, fraction of the time series/per stem in release, and mean duration of release episodes). We compared

these variables between species and the decline levels using ANOVA with the same design used for radial growth. We also calculated the proportion of stems in release at each site at five year intervals, and compared such proportions among species and decline levels with ANOVA in a split-plot design. For both tests, the significance was tested by comparing the F-statistic to the distribution obtained from 10 000 permutations of the proportion of stems in release. For the latter comparison, a Bonferonni correction was applied for multiple testing for the successive tests in the time series.

2.4.4.5 Relative abundance of maple and beech saplings

Factors affecting the relative abundance of maple and beech among saplings were tested using partial Redundancy Analysis (RDA). The dependent variables were, in a first analysis, the maple saplings relative density and basal area (vs. beech) per site, and in a second analysis, the Hellinger-transformed abundances (Legendre and Gallagher, 2001) of all the species recorded among saplings. The independent variables were grouped in four matrices to partition the variance and test for significance (Legendre and Legendre, 1998). The four matrices were: 1) gap history (average proportion of minor release at five year intervals); 2) soil characteristics (first two axes of a Principal Component Analysis (PCA) on base cation availability and the first axis of a PCA on the sand, silt and clay content); 3) composition of the canopy (adult basal area of maple, beech and other species); and 4) other site factors (region and decline). Significance of the partial RDAs was tested against the distribution of the F-statistic after 10 000 permutations of the residuals (Legendre and Legendre, 1998).

All statistical analyses were performed with the R software. Optimization for modelling growth was performed with a quasi-Newton algorithm after an initial search of the parameter space with simulated annealing.

2.5 Results

2.5.1 Sapling age structure

The comparison of the age frequency distribution between species and decline levels indicated a significant interaction between species and decline (Table 2.2, Step 1, χ^2_w =

63.62, df = 43, P = 0.021). Removing the term associated with species-specific age structure [AS] reveals that the difference between species in age structure is highly significant (difference in the χ^2_w = 37.87, df = 8, P < 0.001). However, removing the term associated with decline level-specific age structure [AD] resulted in a non-significant difference between models (difference in the χ^2_w = 14.51, df = 8, P = 0.070).

Both the age structures of maple and beech have an inverse exponential shape and do not reveal any peak in recruitment (Figure 2.1). The age of the saplings for both species ranged between 20 and 100 years old. The most striking result is the dominance of beech in young classes in comparison to maple. Beech had more saplings than maple in the young age classes (20-29 and 30-39 years) in both healthy and declining stands. This difference is opposite to the predicted distribution for these species based on their life-history traits (under a sustainable structure, maple should have a steeper age structure because of its higher mortality rate – Condit et al., 1998; Beaudet et al., 1999).

2.5.2 Growth series

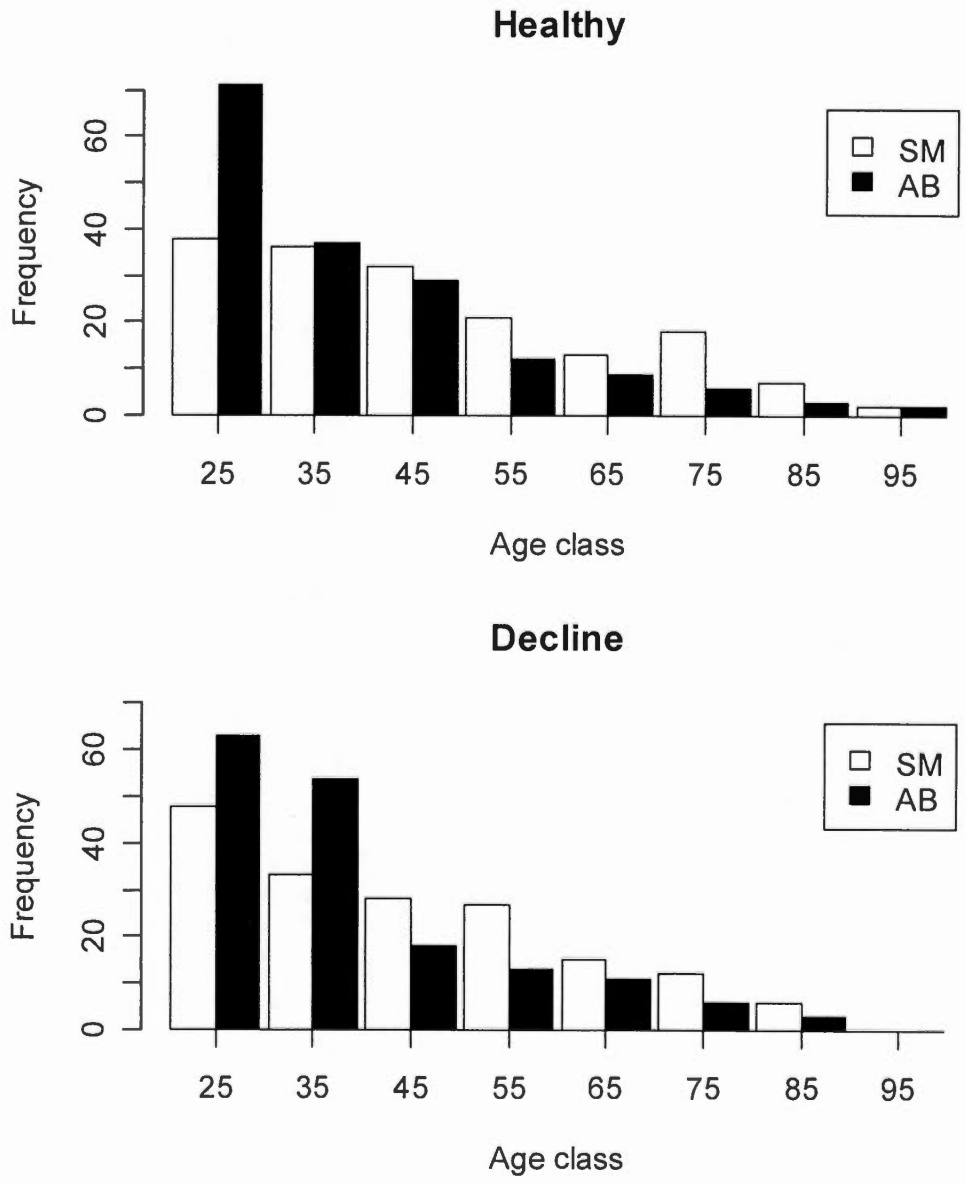
The recent increase of beech over maple in the sapling layer could be related to a major change in growth. Figure 2.2 shows the average radial growth pattern from 1963 to 2003 for maple and beech saplings over 40 years old in healthy and declining stands, indicating a shift in growth hierarchy over time between maple and beech. Maple growth tended to be greater than that of beech prior to 1970, while beech tends to have a greater growth than maple since the 1990's. Differences between decline levels and interactions between species and decline were all non-significant.

Early growth series (first 30 years of development) were compared, within species, between young (<30 years) and old saplings (>50 years) (Figure 2.3). For maple, growth was not statistically different between the two groups of saplings for the first 20 years. However, the growth of young saplings declined in the last 10 years and became significantly lower than that of older saplings. For beech, growth was higher for younger saplings in the 5-15 years after establishment, but did not differ between young and old saplings for the rest of the series.

Table 2.2 Comparison of the age class [A] frequency distributions as a function of species [S] and decline levels [D]. The region [R] is treated as a block. Testing for statistical significance is performed by removing hierarchically terms from a log linear model. The effect of a factor on the age structure is considered significant when the difference in $\square^2_w$ is significant.

Model	Effects in the model	DF	X^2_w	p-value
Full	[A] + [D] + [S] + [R] + [DS] + [AS] + [AD] + [ADS]			
1	[A] + [D] + [S] + [R] + [DS] + [AS] + [AD]	43	63.82	0.021
2	[A] + [D] + [S] + [R] + [DS] + [AD]	51	101.69	<0.001
	Difference model 2 – model 1	8	37.87	<0.001
3	[A] + [D] + [S] + [R] + [DS] + [AS]	51	78.33	0.008
	Difference model 3 - model 1	8	14.51	0.070
3	[A] + [D] + [S] + [R] + [DS]	59	116.16	<0.001
	Difference model 4 - model 2	8	14.47	0.070

Figure 2.1 Frequency distribution of sapling age by stand decline levels. Maple is represented by white bars and beech by black bars. Age classes are midpoints of 10 year classes. Data come from 34 sites divided equally in two decline status. There are respectively 337 and 338 maple and beech saplings.



Various models were fitted to test for a temporal trend in radial growth for maple and beech saplings. The best model of radial growth for maple included terms accounting for a non linear decay of radial growth over time, a linear increase of radial growth with stem radius, a positive response of radial growth to base cation saturation, and suppression and release episodes (Table 2.3, model 10). Adding the decay of radial growth over time improves the fit of the model to the data (model 6 versus model 1). Soil fertility does not have an effect on the growth trend for maple (model 7 versus model 1), but it increases the intercept growth over time (model 10 versus 3). Although they are important factors according to the AIC criteria, the importance of the relation between radial growth and time, size and soil characteristics must however be interpreted with caution because the variance in radial growth explained by these factors is small when the suppression and release history is not taken into account ($R^2 = 0.046$ for the model without suppression and release versus $R^2 = 0.316$ for the best model). Thus, we do present the parameter estimates for the different models.

The best model of radial growth for beech is also a non-linear function of time and stem radius, when the base cation saturation interacts with the growth trend and the suppression and release history (Table 2.3, model 8). Radial growth is declining over time on the least fertile soils (Table 2.3, model 4 versus model 1), although this growth is equal to or greater than that of maple, and it increases over time on the most fertile soils. Base cation saturation does not have an effect on the intercept of the growth over time relation for beech (model 8 versus model 1). Again, even though model comparison with AIC reveals that including time, stem radius and base cations saturation improve the fit of the model to the data, the variance explained by these factors is negligible as shown when suppression and release status is removed from the model ($R^2 = 0.016$ for model 6 versus $R^2 = 0.345$ for the model 8).

Table 2.3 Comparison of saplings growth models for sugar maple and beech. The effect of time and size (stem radius) is tested for a linear and an exponential relationship. The effect of soil (base cation availability) is tested on the intercept of the temporal/size relationship and on its interaction with time (trend). GAP indicates whether the suppression and release status were included in the model. For each species, the best model based on the Akaike Information Criteria (AIC) are in bold.

Species	Model #	Variables in the model							Number of parameters	Maximum Likelihood	AIC	R^2
		Time		Radius		B.S.						
		Exponential	Linear	Exponential	Linear	Intercept	Trend	GAP				
Sugar maple	1	•		•		•	•	•	8	-10563.94	21143.9	0.317
	2		•	•		•	•	•	7	-10570.13	21154.3	0.313
	3	•			•	•	•	•	7	-10564.40	21142.8	0.316
	4			•		•	•	•	5	-10624.05	21258.1	0.268
	5	•				•	•	•	6	-10606.99	21226.0	0.270
	6	•		•		•	•		8	-10811.74	21639.5	0.046
	7	•		•		•		•	7	-10564.02	21142.0	0.318
	8	•		•			•	•	7	-10564.81	21143.6	0.317
	9	•		•				•	6	-10565.86	21143.7	0.316
	10	•			•	•		•	6	-10564.41	**21140.8**	0.316
American beech	1	•		•		•	•	•	8	-10677.33	21370.7	0.345
	2		•	•		•	•	•	7	-10679.41	21372.8	0.343
	3	•			•	•	•	•	7	-10692.09	21398.2	0.329
	4			•		•	•	•	5	-10683.21	21376.4	0.336
	5	•				•	•	•	6	-10751.16	21514.3	0.269
	6	•		•		•	•		8	-10912.64	21841.3	0.016
	7	•		•		•		•	7	-10681.59	21377.2	0.338
	8	•		•			•	•	7	-10677.32	**21368.6**	0.345
	9	•		•				•	6	-10683.48	21379.0	0.335

Figure 2.2 Annual radial growth (5 yr-averages ± 1 S.E.) as a function of time for maple and beech saplings from 17 healthy and 17 declining stands from Quebec. All saplings represented are 41 years old or more. Growth was compared among groups within each 5 year period with an ANOVA. Symbols * denote significant differences between species, within a 5 year period, at 0.05 level after Bonferonni correction for multiple testing. Differences between decline levels and interactions between species and decline were all non-significant. Years correspond to the 5 year period midpoint.

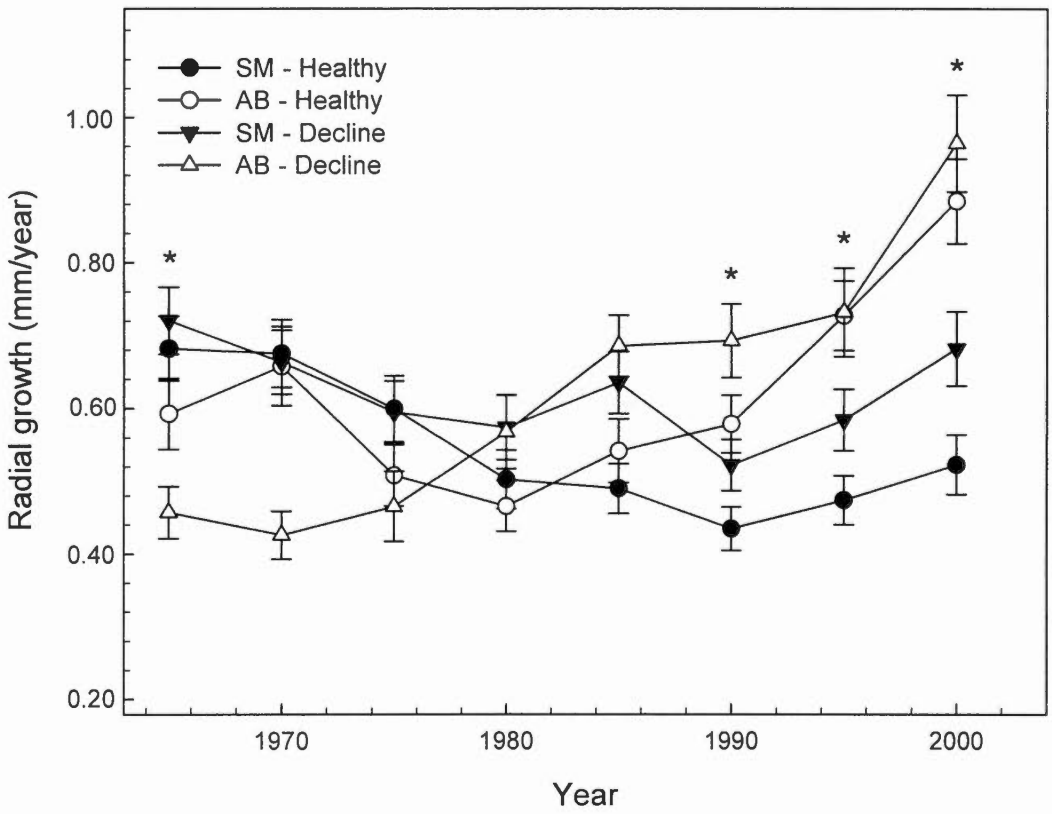
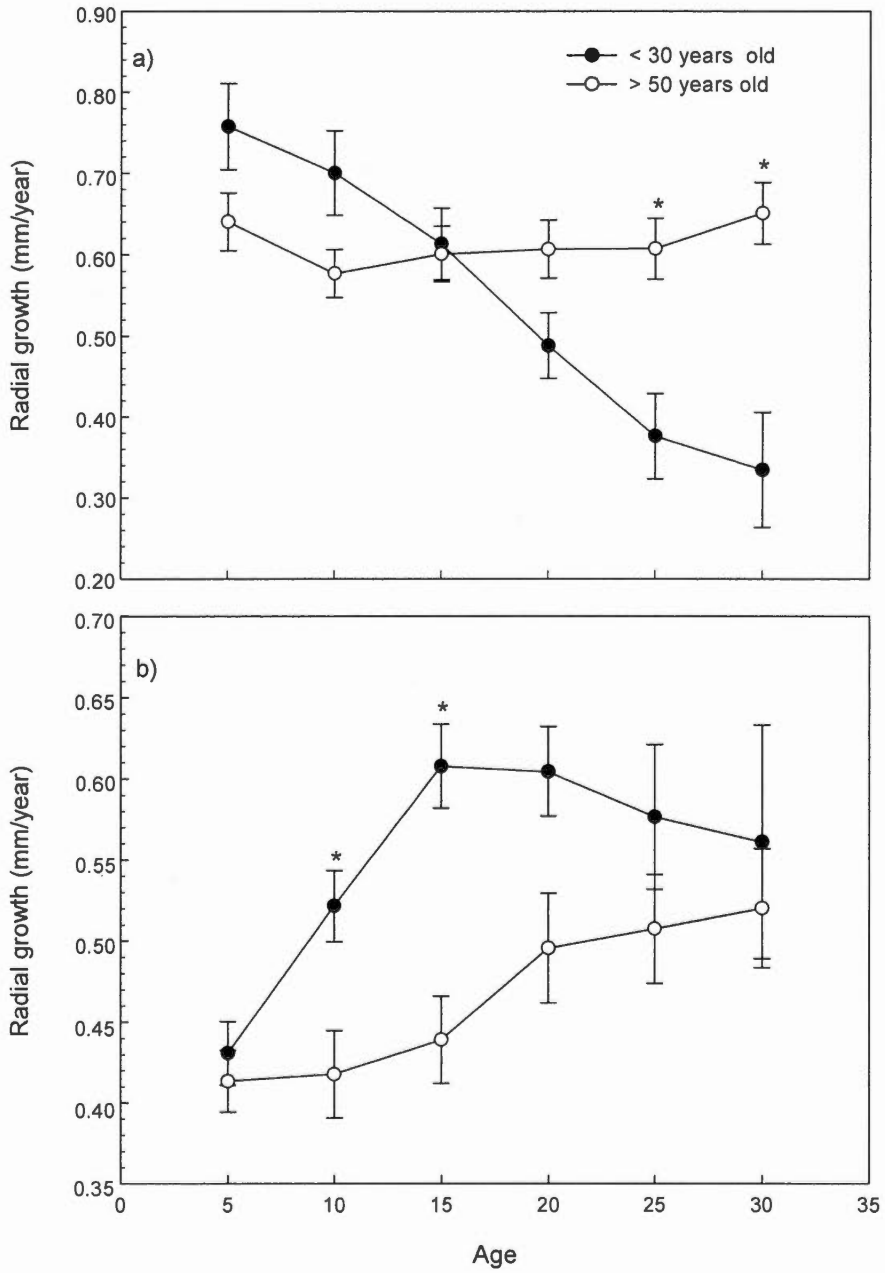


Figure 2.3 Comparison of early (first 30 years) radial growth for a) maple and b) beech. Full and open symbols correspond to saplings < 30 years old and > 50 years old in 2003, respectively. Growth is averaged by 5 year period and comparisons by ANOVA were performed within each 5 yr period. Symbols * denotes significant differences between series at 0.05 level after Bonferonni correction for multiple testing. Error bars are ± 1 S.E.



2.5.3 Suppression and release history

Suppression and release history is the factor explaining the most variance in sapling radial growth. We first tested differences in the descriptors of suppression and release history (number of releases per series, fraction of time in release and average release duration) and found no major differences between species and decline levels (Table 2.4). The only statistically significant difference was a greater number of minor and major releases per series for maple (repectively $P = 0.003$ and $P = 0.039$), however, the magnitude of the difference was marginal (Table 2.4).

The proportion of stems under minor release (and also major release, not shown) followed a marked non-linear pattern over time (Figure 2.4). There were no significant differences between species or decline classes. The proportion of stems in minor release ranged between 50 and 60% for the 1960's decade, it decreased to 20-35% in the 1980's, and then increased in the 1990's to 50-60% during the period of 1998-2003. The pattern is U-shaped for both species. When a polynomial was fit to the data (results not shown), much of the variance was captured by the second degree term, describing this U-shape.

2.5.4 Sapling composition

We did multivariate analyses to partition the variance in sapling composition as a function of site and environmental characteristics. The first RDA performed on the relative abundance of maple calculated from both sapling density and basal area revealed the proportion of minor releases (35.2% of the variance, Table 2.5) as the factor that explained the most variance, followed by the region and decline (17.1%). The analysis combining all factors was weakly significant ($P = 0.056$, $R^2adj = 0.336$), but all the partial analyses were not significant. This might be explained by the presence of colinearity between the five year periods of minor release frequency. Maple relative abundance was positively correlated to the proportion of stems in minor release during the 1975, 1980 and 1985 periods, but negatively correlated to the 1965, 1970 and 1995 periods (Figure 2.5). This result shows that the relative abundance of maple is affected by the pattern of the proportion of stems in minor release shown in the Figure 2.4. The ordination of the proportion of release at five-year intervals

Table 2.4 Descriptors of minor and major release events identified in 41 year-long growth series of sugar maple (SM) and American beech (AB) saplings in sugar maple stands with healthy or declining status (in the 1980's). Summary of ANOVA results are presented at the right (see text for details). P values < 0.05 are in bold.

			Healthy stands (mean ± 1 S.E.)	Declining stands (mean ± 1 S.E.)	Effect comparison (P-values)		
					Species	Decline	Species X Decline
Minor release (>100%)	Nb release events	SM	2.07 ± 0.07	1.97 ± 0.08	**0.003**	0.561	0.589
		AB	1.74 ± 0.07	1.72 ± 0.08			
	Fraction of series in release	SM	0.39 ± 0.01	0.40 ± 0.01	0.061	0.376	0.667
		AB	0.37 ± 0.01	0.37 ± 0.01			
	Release duration (yr)	SM	8.47 ± 0.30	9.67 ± 0.38	0.257	0.111	0.200
		AB	9.77 ± 0.42	10.02 ± 0.43			
Major release (>200%)	Nb release events	SM	1.86 ± 0.08	1.93 ± 0.08	**0.039**	0.369	0.736
		AB	1.58 ± 0.09	1.71 ± 0.09			
	Fraction of series in release	SM	0.26 ± 0.01	0.27 ± 0.01	0.295	0.301	0.523
		AB	0.26 ± 0.01	0.28 ± 0.01			
	Release duration (yr)	SM	5.60 ± 0.15	5.54 ± 0.15	0.829	0.576	0.491
		AB	5.88 ± 0.19	6.05 ± 0.22			

Figure 2.4 Variation over time in the fraction of maple and beech saplings under minor release (> 100% increase in radial growth) in stands with healthy vs. declining status in the 1980's. Fractions were determined annually but then averaged over 5 yr-periods and compared by ANOVA for each 5 yr period. After Bonferonni correction, there were no significant differences among species and decline level, neither significant interactions.

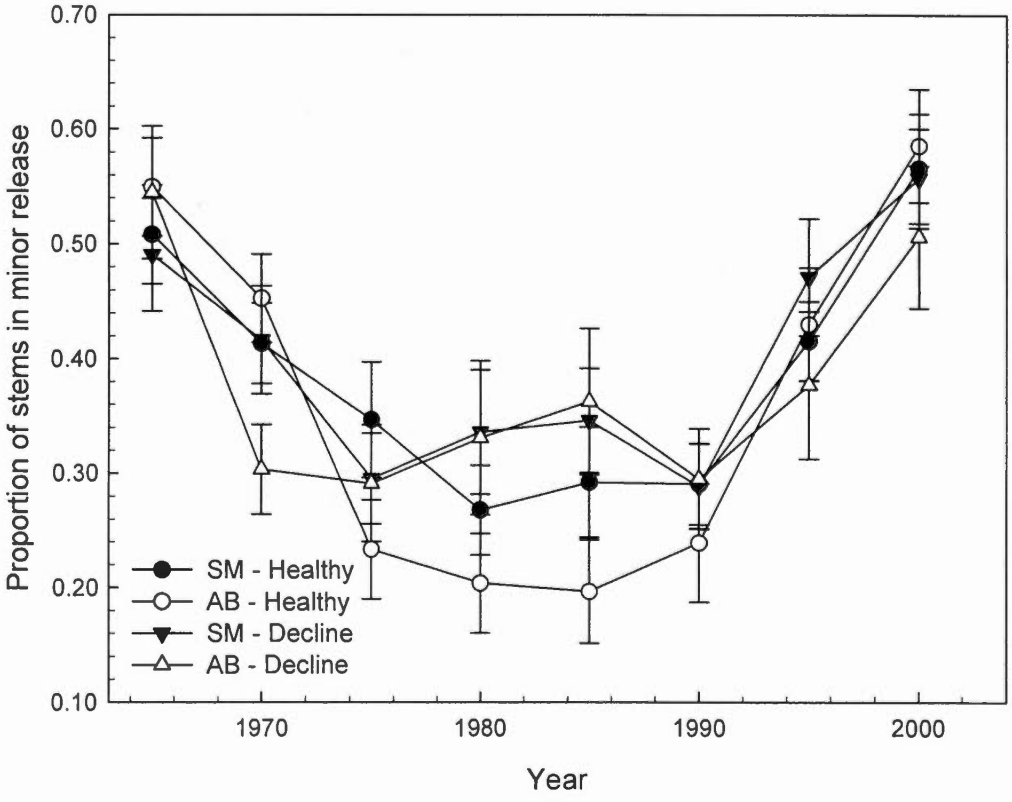
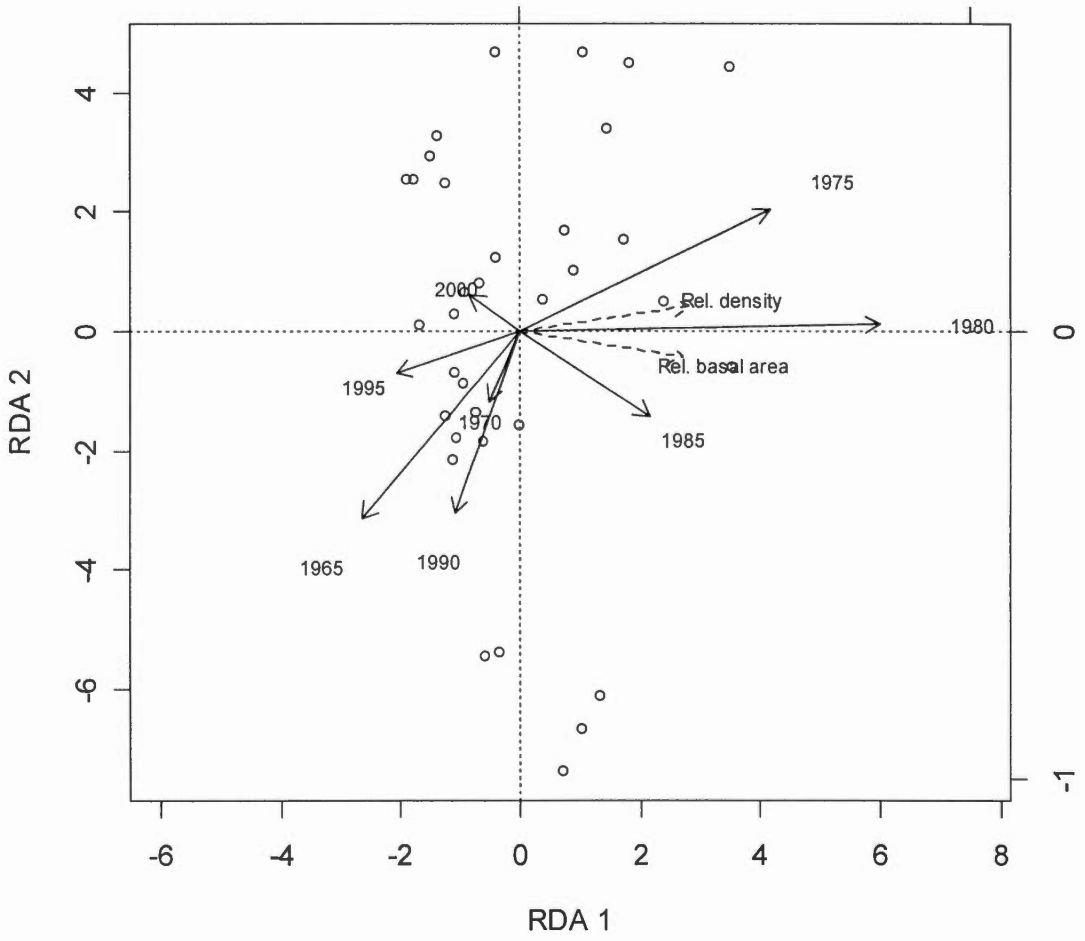


Table 2.5 Summary of the variance partitioning of saplings abundance by partial Redundancy Analyses. Details on the content of each matrix of explanatory variables are given in the text.

Explained variables	Matrices of explanatory variables	Partial R^2	Partial adj. R^2	P-value
Maple relative abundance (from density and basal area)	All factors	0.658	0.336	0.0555
	Soil properties	0.054	-0.011	0.4183
	Canopy composition	0.086	0.042	0.2714
	Minor release frequency/ 5 year period	0.428	0.352	0.0812
	Region and decline	0.139	0.171	0.0913
All species abundance (Hellinger distance transformation)	All factors	0.627	0.276	0.0023
	Soil properties	0.104	0.063	0.1756
	Canopy composition	0.113	0.077	0.1379
	Minor release frequency/ 5 year period	0.256	0.106	0.1560
	Region and decline	0.116	0.126	0.0484

Figure 2.5 Biplot of partial redundancy analysis of maple relative abundance among saplings (calculated against beech absolute density and basal area) as a function of the proportion of all stems (maple and beech combined) in minor release by five years period. The matrix of covariables includes soil variables, canopy characteristics and site factors (see text for a list of the variables included).



(Figure 2.5) illustrates the contrast between the 1975-1985 periods and the remaining time periods. The more stems in release in the 1975-1985 period, the more abundant maple was relative to beech. A RDA was also performed on all species abundance in the sapling layer, however, the pattern was less clear than with the previous analysis (ordination not shown). The overall proportion of the variance explained in that analysis was 27.6% (P = 0.002). The region and decline status explained the largest part of the variance (12.6%, P = 0.048), followed by the proportion of stems in minor release (10.6%, P = 0.156). The abundance of sugar maple was orthonormal to that of *Acer pensylvannicum* L., and weakly negatively correlated to that of beech, *Acer spicatum* Lam., and *Betula alleghaniensis* Britton. The abundance of maple was positively correlated with the proportion of stems in release during the 1975-1985 period, and beech was positively correlated to the 1965-1970 period.

2.6 Discussion

The main objective of this study was to explain the recent regional increase in the relative abundance of beech saplings by looking at the age structure, temporal growth patterns of saplings (release event history and growth trend), and the factors explaining variation among sites in sapling relative abundance. The mechanisms explaining these fluctuations in the relative abundance of maple and beech at the scale of a single stand are well documented (see the Introduction). At the regional scale (southern Quebec), however, mechanisms responsible for the fluctuations must be different (Leibhold et al., 2004). Our results showed that the actual sapling age structures for maple and beech did not correspond to the structures that would be predicted under steady-state dynamics. The high abundance of beech relative to maple observed in the young age classes suggests that there has been a decline in the establishment or in the survival of maple relative to beech. We also found a shift in radial growth hierarchy between these two species in the 1980's. The beech sapling population has been surpassing maple in growth since 1990's, although it showed greater growth in the 1960's. A discussion follows regarding the three main hypotheses proposed to explain the recent increase in beech abundance and growth: response to base cation leaching, canopy opening following the 1980's maple decline episode, and a change in the suppression and release dynamics at the regional scale.

2.6.1 Response to base cation leaching

Recent base cation leaching on some sites has been hypothesized as being responsible for changes in the recruitment dynamics of maple and beech (Kobe et al. 2002; Lovett and Mitchell 2004; Duchesne et al., 2005). It was a very likely explanation for the observed increase in beech relative abundance among saplings when this study was initiated. The depletion in soil base cation consequent to important sulphur and nitrogen deposition since the 1950's is well documented in northeastern North America (see reviews by Driscoll et al. 2001; Tomlison 2003). There have been numerous studies that showed that maple is nutrient demanding (e.g. Bernier et al., 1989; Horsley et al., 2000; Drohan et al., 2002) and growth declines have been presumed to be a response to base cation leaching (e.g. Ryan et al., 1994; McLauglin, 1998; Watmough, 2002; Duchesne and Ouimet, 2002). Moreover, controlled experiments have demonstrated sensitivity of both seedlings and adults to simulated acidic depositions (Fyles et al., 1994; Long et al., 1997; Moore et al., 2000; Kobe et al., 2002; St-Clair et Lynch, 2005; Juice et al., 2006). In agreement with all of these evidences, simulations with a forest dynamics model predicted an increase in beech and a corresponding drop in maple on a time scale of 125 years under simulated base cation leaching (Kobe et al., 2002). However, contrary to these results and to our initial hypothesis, the signs of regeneration failure and the declining growth observed in maple were not related to soil status, but rather were found in almost all conditions from both regions investigated.

The recruitment dynamics of maple and beech appears more complex than predicted by only a base cation leaching phenomenon. At the regional scale studied here, and under a constant environment scenario, we would expect to find a balanced age-structure which would correspond at equilibrium to each species' traits. A greater representation of maple relative to beech would therefore be expected in the young age classes due to maple's lower survival (Condit et al., 1998). The observed age structures however did not agree with the expected ones, being characterized by an over-representation of beech in the 20-40 years old age classes. The presence of higher than expected beech densities was not restricted to a single age class, which leads us to reject the hypothesis of a pulse of establishment in beech associated with one or a few exceptional mast crops. Although base cation leaching could be responsible for this pattern, there are other causes that might also be involved. For instance, it has been shown that in an old-growth forest, the shade of the understory was too deep for

successful recruitment of maple, leading to an increase in beech (Beaudet et al., 1999). In the stands sampled here, a heavy suppression period from 1975 to 1990 could have created a similar pattern. Moreover, maple might suffer from increasing competition from understory beech, either because beech intercepts light effectively (Canham et al., 1994; Hane, 2003), impacts local soil properties (Finzi et al., 1998; Dijkstra et al., 2001) or could have allelopathic effects on maple seedlings (Hane et al., 2003).

The second prediction of the base cations leaching hypothesis is the presence of a decline in maple sapling growth that would be associated with a lower base cations availability, while a neutral growth trend is predicted for beech. The demographic consequence of a decreasing growth rate is a lower transition rate from the seedling to the sapling stage. A lower growth is also associated with a higher probability of mortality (Kobe et al., 1995). Looking only at the mean growth series over time, beech started to depart from maple with a higher growth in the 1990's, whereas maple growth was superior or equal to that of beech from 1965 to 1985. The change in the growth hierarchy between the two species was in fact mostly due to the recent increase in the growth rate of beech. The comparison of growth models (Table 2.3) showed how numerous factors interact to affect and determine the average observed growth trend over time (Figure 2.2). However, the growth of maple was not related to soil characteristics as was expected under the base cation leaching hypothesis (Table 2.3). Moreover, the fraction of the total variance in annual growth explained by the temporal trend and size effect was negligible relative to the fraction explained by the suppression/release status. Thus, the declining growth trend must be interpreted with caution and the emphasis must be given to the temporal pattern of suppression and release.

The comparison of early growth series for stems < 30 years old with those of stems > 50 years old in 2003 supports our rejection of the base cation leaching hypothesis. As explained earlier, an increased risk of mortality among stems with lower growth rates (Kobe et al., 1995) should result in older surviving stems having, on average, a greater growth early in their life history than young stems (Landis and Peart, 2005). A greater growth would also be expected among the stems established before the base cation availability was affected by acidic deposition. The above predictions were clearly rejected for beech, for which early growth was the same for both young and older saplings, with even superior growth for

saplings <30 years old in some age classes. The pattern was less clear for maple, but still, with the exception of the last two age classes, the early growth series were not significantly different. We interpret this comparison as evidence that young maple and beech stems are more vigorous than what would be expected under a constant rate of gap formation and a strong effect of declining base cation availability. We suggest the late growth decline of maple among the young stems could be attributed to increasing competition by beech following its recent increase in sapling density (approximately 1900 stems/ha in the studied stands) and growth vigour. Therefore, although we cannot definitively reject the hypothesis that base cation leaching had an impact on saplings dynamics, we conclude that changes in the saplings release history had a much more important impact on the demography of the species.

2.6.2 Canopy opening following maple decline episode

Duchesne et al. (2005) hypothesized that the recent increase in beech sapling abundance relative to maple could be a response to the maple decline episode that started in the 1980's. The authors reported a correlation between the nutritive status of mature maple trees and the demographic increase of beech observed in various stands. They suggested that beech growth increased in response to the opening of the canopy in stands affected by maple decline. However, they did not observe a significant correlation between measurements of canopy openness and the increase of beech. Here, our results have shown that variation among stands in the relative abundance of maple was best explained by the release history (i.e., the proportion of stems in release). We did not find any relation between the decline episode and the proportion of stems in release. Moreover, we showed that the proportion of stems in release was the lowest during the period corresponding to the reported decline episode. We did not find a relation between the presence of the decline status of the stands and the sapling age structure and abundance. Such results therefore do not support the hypothesis that the recent increase of beech relative to maple would result from the opening of the canopy associated with the 1980's maple decline episode.

2.6.3 Temporal pattern of suppression and release

This study revealed a pronounced variation in the release frequencies over time, with higher frequencies in the 1960's and 1990's and lower frequencies during the 1970's and 1980's. This U-shape temporal pattern was consistent among sites, with no distinction between regions, decline status or species. We do not know of any study documenting similar patterns at such a large scale. This synchrony among sites and regions suggests the presence of a climatic or human influence. Variations over time in the proportion of stems in release might occur as a result of random or cyclic processes, or as a result of a directional trend due to forest succession. Potential causes are multiple, possibly additive and could have impacted different time periods. For instance, it could be related to changes in the logging practices over time (with the possibility of periods with higher harvesting rates synchronized across regions), the occurrence of extreme climatic events (e.g. severe ice storm [Rhoads et al., 2002], severe drought [Payette et al., 1996; Olano and Palmer, 2003]), climate change and insect outbreak (Payette et al., 1996). We could not identify any factor from our data causing this pattern; therefore we will restrict our discussion to the interpretation of the dynamics following such a change.

Light availability is a major niche axis differentiating these species (Pacala et al., 1996) and obviously fluctuations in light availability would result in corresponding fluctuations in recruitment dynamics. The traditional model for coexistence of maple and beech (Poulson and Platt, 1996) predicts that under elevated light conditions it is likely that maple will have a greater recruitment (in absolute number of individuals) than beech because of its greater fecundity and known ability to maintain an abundant seedling bank (Graber and Leak, 1992; Ribbens et al., 1994). Under low light conditions, mortality is expected to be higher for maple than beech (Kobe et al., 1995). During periods when low light conditions predominate, both species should decrease in density, but the decline should be slower for beech due to its higher survival under low light (Kobe et al., 1995), and this species should therefore increase in relative abundance. In this study, the relative abundance of maple was mostly associated with the temporal pattern of the proportion of stems in release. The lower frequencies of release observed in the 1975-1985 period seems to limit the current abundance of maple. An increase in maple mortality in the shadiest sites during this period would be consistent with the studies cited above.

Our results suggest that beech had a more favourable response than maple to the rising frequency of release during the 1990 to 2000 period. Increased growth during that period for beech probably allowed a rapid transition from the seedling to the sapling stage, a possible explanation for the doubling of beech density in the last 10 years recorded in the Quebec forest inventory data (Gravel et al., in prep) and as reported by Duchesne et al. (2005). It is less clear why maple did not follow a similar increase during this period. The conceptual model of Poulson and Platt (1996) predicts the response of maple to elevated light conditions should be greater or at least similar to that of beech. However, the relative deficiency of young maple and the negative correlation between maple relative abundance and release frequency in the 1990's are contrary to this prediction.

Although it is probably not possible to identify the cause(s) that may have prevented maple from benefiting demographically from the increased release frequency in the last 15 years from of the data presented in this study, our results nevertheless allow us to suggest some hypotheses. We showed a recruitment failure for maple in the last 40 years, but it remains difficult to determine if it resulted from establishment limitations (fecundity and germination) or from an increased rate of sapling mortality. The decrease in growth of young maple sapling illustrated in Figure 2.3 would suggest a decrease in vigour and presumably a corresponding increase in mortality (Kobe et al., 1995). As mentioned above, this could be the result of an increase in competition from beech saplings. This pattern is somewhat similar to what was observed in an old-growth forest in Quebec (Beaudet et al., 1999). Extended low light conditions at that site resulted in recruitment failure of maple in the sapling layer, despite extremely high densities of seedlings for this species and a rich soil with elevated base cation saturation. In 1998, a major ice storm affected the canopy leading to a sudden increase in understory light availability, but no shift in the species hierarchy was observed (Beaudet et al., 2007). In agreement with these results, we hypothesize that extended low light conditions during the 1980's reduced maple abundance among saplings more than beech, and thus affected the ability of maple to respond to the canopy opening during the 1990's. On the other hand, beech was not as much affected by the conditions during the 1980's and benefited from the opening of the canopy to increase in abundance during the

1990's. Consequently, direct competition from beech increased (Hane, 2003; Hane et al., 2003) and prevented further the establishment of maple during this period.

2.7 Conclusion

This study revealed that temporal variations in release frequency occurring at the regional scale had a major impact on recruitment dynamics of maple – beech forests. We suggested this pattern could result from the interplay of different factors such as past logging history, extreme climatic events or insect outbreaks. Our results indicate that if there was any effect of base cation leaching on sapling dynamics, the effect was not as great in magnitude as that of canopy disturbance. Moreover, the hypothesized role of the sugar maple decline episode during the 1980's in explaining the current dynamics was clearly not supported by our findings.

Forest communities are never totally in balance at the scale of a single stand (Poulson and Platt, 1996; Woods, 2000), but this could also be true at the regional scale. The conceptual models of coexistence in these communities account for variations through time in the rate of canopy gap formation at the scale of the stand. But links between stand-scale rates of gap formation and larger-scale variations in disturbance regimes are less well understood. Disturbance regimes are known to result from the complex interplay of allogenous and exogenous factors, and there are obviously many potential processes at the regional scale that could affect the latter. Future research should aim at better identifying such factors, and better understanding how they might affect disturbance regimes and forest dynamics at multiple spatial and temporal scales.

2.8 Appendix : Description of the method used to identify release episodes, and comparison with different published methods

It was assumed that a sapling baseline radial growth (called here low light radial growth, LLRG, the terms between square brackets in Eq. 1) is increased suddenly for a short period of time by canopy gaps. The radial growth of a sapling periodically subjected to small scale disturbances can be described conceptually as:

Eq. A.1 Radial growth = (GAP+1)*LLRG

The 28 objective methods reviewed by Rubino and McCarthy (2004) are essentially variants of three main types of methods. The first method ('static') is the comparison of annual growth to a fixed criterion. A release event is detected when growth is superior to the criteria for a minimum period of time (number of consecutive years). The second type of method involves detecting a sudden increase of growth by comparing average growth of two consecutive periods of time. A release is detected when the average growth from one period of time is superior by a certain relative amount to the one during the precedent period. Finally, standardization and detrending procedures look at the series after it has been divided by the mean or the trend (linear or not). Release events are detected by the presence of sustained periods of growth superior to the mean or the trend. The rationale for using a given technique for identification of release events depends on the goal of each specific study. Here, we are interested in taking into account and identify long term trends in baseline growth rate, as well as to determine how the duration and frequency of release events vary over time. The presence of a pronounced temporal trend in the growth series will affect the capacity of the fixed criteria and the standardization methods to identify release events either at the beginning or the end of a series because the growth increase threshold does not vary over time. The detrending procedure will be sensitive to the occurrence of a release event at the beginning or the end of a series because the trend is evaluated prior to the release event, and thus the release event will bias the evaluation of the trend. Finally, the running mean method has the disadvantage of requiring the truncation of the series at the beginning and the end because for the calculation of the running mean. For instance, with a time window of 4 years, this mean the series of 41 years must be truncated of 4 years at the beginning and 3 years at the end.

A method based on a maximum likelihood estimation was here developed to identify release events based on Eq. 1. The method is conceptually similar to the detrending procedure where the release events are identified as sustained departures from the trend. The difference between the detrending method and the method used here is that here, rather than being evaluated in two separate steps, the trend and the release events are evaluated simultaneously. The final solution maximizes the sum of the log-likelihood (SLL) considering both the trend and the suppression/release history. A linear growth trend is assumed to avoid overfitting. This iterative method follows this procedure: 1) A suppression/release history vector with the same length as the series is created to record for each year the value of the categorical variable GAP (0, 1 or 2). The initial vector is a null vector (all 0); 2) The growth trend parameters of the series (intercept and slope) are evaluated by maximizing SLL, considering the suppression/release history vector and Eq. 1, and the SLL is recorded; 3) A unit vector of 4 elements long (called GAP vector, where all entries are 1, coding for minor release) is placed at the beginning of the suppression/release history vector; 4) The step 2) is calculated and the SLL is compared to the precedent SLL. The solution is recorded (SLL and suppression/release history) if the SLL is higher than the precedent; 5) The steps 2-4 are repeated for all possible locations of the GAP vector on the suppression/release history vector; 6) The steps 2-5 are repeated for additional GAP vectors until all permutations of suppression/release history have been assessed; 7) The steps 2-6 are repeated with a GAP vector coding for major release (all entries are 2), for the optimization of the major release series. At the end of the procedure, the maximum SLL, the intercept and the slope, and the suppression/release series are recorded.

The performance of the maximum likelihood and the traditional methods described above to identify suppression and release history and growth trend were compared for the 25 sub-sampled series using the Akaike Information Criteria (AIC). We used the mean growth of the sub-sample population as the fixed criteria (0.606 mm/year). A minor release is detected by the occurrence of at least 4 consecutive years of growth superior to this criteria by 100% and a major release by growth superior by 200%. The second method is the running mean with a 4 year window. A minor release is detected by an increase by 100% of growth in a 4 years window relative to the precedent 4 years window. A major release is an increase of

200%. The third method is the standardization method. The series is divided by its mean and minor and major release events correspond respectively to a period of 4 years or more of growth that is superior by 100% and 200% to the mean. The fourth method is the detrending method. The linear trend is first calculated and minor and major release events corresponding respectively to a 4 year or more period of growth that is 100% and 200% over the trend. After the evaluation of the suppression and release history with all the methods, the series and their respective suppression and release codification have been truncated by removing the 4 first years and the last 3 years to match the period covered by the running mean method. The growth trend was then evaluated by maximizing the SLL giving a linear growth trend of LLRG and the suppression and release status with a normal distribution of the residuals. The AIC was calculated for all series and methods. The maximum likelihood estimation method was the best method according to the AIC criteria (see Table 2.1) and therefore identification of release events was performed on our 481 growth series using this method.

Table 2.1A Comparison of the different methods to identify release episodes. The analysis was performed on a sub-sample of 25 growth series of 41 years. See text and the appendix for details.

	Technique to identify release episode				
	Departure to the mean	**Departure to the trend**	**Fixed threshold**	**Moving average**	**Maximum likelihood estimation**
Mean AIC	491.87	495.27	492.08	487.56	479.79
Number of series (out of 25) for which the method was the best	3	0	3	7	14
Average percent of time in suppression	0.962	0.984	0.897	0.366	0.618
Average fraction of time in minor release	0.034	0.017	0.085	0.249	0.179
Average fraction of time in major release	0.004	0.000	0.019	0.385	0.204

CHAPITRE III

RECONCILING NICHE AND NEUTRALITY : THE CONTINUUM HYPOTHESIS

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3.1 Résumé

Dans cette étude, nous posons la question si, plutôt que d'être fondamentalement opposées, les théories niche et neutre sont simplement situées aux deux extrêmes d'un continuum. Premièrement, nous présentons un modèle de probabilités de recrutement qui combinent à la fois les processus niche et neutres. À l'aide de ce modèle, nous prédisons et testons si l'importance relative des processus niche et neutre dans leur effet sur la dynamique des communautés va varier avec la richesse en espèces, la superposition des niches et les capacités de dispersion des espèces (courte et longue distance). Les résultats démontrent que la niche et la neutralité représentent les deux extrêmes d'un continuum allant de l'exclusion compétitive à l'exclusion aléatoire. En absence d'immigration, l'exclusion compétitive tend a créer un espacement régulier des niches. Néanmoins, l'immigration prévient l'établissement d'une limite à la similarité. La communauté à l'équilibre est constituée d'un agencement d'espèces complémentaires et redondantes, avec leur abondance déterminée respectivement par la distribution des conditions environnementales et par l'intensité de l'immigration.

Mots clés : Hypothèse du continuum, modèle de loterie, modèle neutre, niche, distribution d'abondance relative, SORTIE-ND

3.2 Abstract

In this study, we ask if instead of being fundamentally opposed, niche and neutral theories could simply be located at the extremes of a continuum. First, we present a model of recruitment probabilities that combines both niche and neutral processes. From this model, we predict and test whether the relative importance of niche vs neutral processes in controlling community dynamics will vary depending on community species richness, niche overlap, and dispersal capabilities of species (both local and long distance). Results demonstrate that niche and neutrality form ends of a continuum from competitive to stochastic exclusion. In the absence of immigration, competitive exclusion tends to create a regular spacing of niches. However, immigration prevents the establishment of a limiting similarity. The equilibrium community consists of a set of complementary and redundant species, with their abundance determined respectively by the distribution of environmental conditions and the amount of immigration.

3.3 Introduction

A central goal of community ecology is to predict the distribution and abundance of species in space and time. Two distinct families of theoretical models have been developed toward this end. Models of niche differentiation are the basis for the vast majority of coexistence theories and have been used to explain the distribution and abundance of a wide range of taxa in both terrestrial and aquatic environments (see Silvertown 2004 for a review). The second type of model invokes species that are ecologically equivalent and a dynamics governed by stochastic processes of extinction, immigration and speciation (Hubbell, 1997; 2001; Bell, 2000). The latter models have attracted enormous attention among ecologists because of their surprising simplicity, the apparent accuracy of their predictions for some taxa (Bell, 2001; Hubbell, 2001; Volkov et al., 2003; He, 2005) and their highly controversial assumption of species equivalence (Whitefield, 2002; Gaston and Chown, 2005). Despite the general agreement that neutral models can predict some aspects of diversity patterns as well or better than previous models (Volkov et al., 2003), they have also raised considerable disagreement (Chase, 2005). Each type of models has limitations that have been widely discussed (Chesson, 2000; Hubbell, 2001; 2005; Chave et al., 2002; Chave, 2004; Tilman, 2004; Gaston and Chown, 2005; Chase, 2005).

The neutral model is commonly perceived as a null alternative to niche theory (Harte, 2004; Gaston and Chown, 2005). Tests of the neutral model initially focused on simply comparing empirical patterns of species distribution to the patterns predicted by the model (Bell, 2001; Hubbell, 2001; Condit et al., 2002; McGill, 2003a; Volkov et al., 2003). This approach has been strongly criticized (Nee and Stone, 2003; Chave, 2004; McGill, 2003b), and subsequent studies have sought to highlight differences in the predictions of the two alternate models and test them simultaneously. Tests of the alternate models have been conducted in a wide variety of ecosystems, including tropical forests (Hubbell et al., 1999; Duivenvoorden et al., 2002; Potts et al., 2002; Tuomisto et al., 2002; Hardy and Sonké, 2004; Svenning et al., 2004; Uriarte et al., 2004), temperate forests (Clark and McLachlan, 2003; Gilbert and Lechowicz, 2004), grasslands (Fargione et al., 2003; Adler, 2004) and marine ecosystems (Wooton, 2005). While some of these tests tended to support either niche or neutral models, in most cases the results were intermediate between the two.

Inconclusive results present a challenge from the strict sense of hypothesis testing. It may be that methodologies or datasets were not adequate to allow a critical test of the differences between the models. An alternative explanation is that both niche and neutral processes operate in any community. This view appears to be implicitly shared by many ecologists (Hurtt and Pacala, 1995; Hubbell, 2001; Chase and Leibold, 2003; Barot, 2004; Gaston and Chown, 2005), but has not yet been formally incorporated in models that can explore the relative importance of niche vs. neutral processes.

The processes of the neutral model are birth, death, dispersal and speciation (Hubbell, 2001). The model assumes that all species of a community are equal in their traits regarding these processes. As a result, species follow a random walk to extinction (ecological drift). Niche differentiation will impact any of these processes because of distinct relationships with environmental factors (biotic and/or abiotic) and will produce correlations between the species abundance and environment. In this study we present a simple, unified model of recruitment processes (dispersal and birth) in which both niche and neutral processes are present and where the relative importance of each varies along a continuum. In our model – inspired by Hurtt and Pacala (1995), Hubbell (2001) and Tilman (2004), among others – recruitment is a lottery function of both interspecific differences in competitive ability (niche process) and of local and long distance dispersal limitations (neutral processes). We compare the recruitment probabilities expected for the neutral recruitment model, the niche recruitment model and the unified recruitment model. For simplicity, we assume species are equal in their death probability, although it is obvious that differentiation could also occur through this process. The models also focus on the local community scale. Thus, we do not consider speciation, and we recognize that further work is necessary to unify the models at the metacommunity scale.

Our first objective is to identify the factors – or more specifically the community characteristics – that will determine where on this continuum from niche to neutrality a particular community will lay. Our second objective is then to assess how the distribution of relative abundance of species, and their distribution and organization along environmental gradients, are affected by the relative importance of niche versus neutral processes. We will first present a simple non-spatial analysis for a two-species community and examine how

variation in competitive inequality and local and long distance dispersal are sufficient to create the continuum from niche to neutrality. Then, we extend the analyses to more complex situations with spatially-explicit simulations of species-rich communities in a heterogeneous environment.

The first prediction we will test is that the "neutrality", i.e. the ecological drift, of a community increases with species niche overlap. Second, we predict that neutrality increases with species richness, because of (a) increasing richness along a finite environmental gradient implies an increasing species packing along the gradient (and thus potentially a greater fundamental niche overlap) and (b) because of an inverse relation between average population size and richness in a community of fixed size (and thus dispersal limitation). Third, we predict a positive relationship between neutrality and dispersal capabilities. Increasing dispersal abilities increase the relative abundance of inferior competitors in the local propagule supply (from source populations elsewhere in more favourable sites in the neighbourhood or the region), and thus decrease the impact of species inequalities. Finally, we expect following Tilman (2004) that in the absence of immigration, diversity will stabilize once a limiting degree of similarity is reached. However, we predict that immigration would counteract the limiting similarity by constantly rescuing rare species from stochastic extinction, thus increasing the neutrality of the local community.

3.4 Model description

3.4.1 Recruitment under neutral and niche processes

Recruitment of new adults in our model follows the lottery process of Hubbell's neutral model (Hubbell, 1997; 2001), to which we add niche differentiation in a spatially heterogeneous environment. Recruitment events only take place following the death of an adult, because of intense competition for space. At each time step, a certain fraction of adults dies at random and is replaced by recruits originating from either the local community or by immigration from the metacommunity. The probability that an adult will be replaced by a particular species in Hubbell's neutral model is given by the species' relative abundance at both local and regional scales (i.e. the metacommunity):

Eqn. 1.

$$R_i = (1-m)\left(\frac{N_i}{J}\right) + m(P_i)$$

where parameter m is the probability that a recruit is an immigrant coming from the metacommunity. The first term is the contribution of the local population of species i to the propagule supply, given by its abundance N_i over the size J of the local community. The second term is the contribution of the metapopulation of species i to the propagule supply, given by its relative abundance P_i in the metacommunity.

Hubbell's neutral model is spatially implicit because it distinguishes the local community and the metacommunity. This poses the problem of defining the boundaries of the local community and assuming uniform dispersal within this community. The model can be made more spatially explicit by recasting it in terms of dispersal processes. At a given replacement site, the composition of the propagule supply is the result of the dispersal from parents, regardless of whether they are "local" or "regional" individuals. A spatially-explicit but neutral model of recruitment then takes the form:

Eqn. 2.

$$R_i = \frac{\sum_{r=1}^{n} N_{i,r} W(r)}{\sum_{j=1}^{s} \sum_{r=1}^{n} N_{j,r} W(r)}$$

where the recruitment probability of species i is the sum of its propagules coming from N conspecific adults located at all r distances, weighted by the dispersal function W(r), divided by the sum of the propagules coming from adults of all s species at all r distances. Modelling the recruitment probability with a local dispersal kernel avoids the need to define boundaries for the local community because each replacement site has its own neighbourhood. However, it could include immigration from a metacommunity. A typical dispersal kernel is usually a steeply decreasing function of distance, but with a long "fat" tail (Nathan and Muller-Landau, 2000). The area under the remote part of the tail corresponds conceptually to the contribution

of the metacommunity to the propagule supply through long distance dispersal (i.e. immigrants). Therefore, immigration can be modelled with a continuous kernel when one has an exact image of the metacommunity and the fat tail of the kernel; otherwise it can be approximated by modelling a quantity of immigrants in the propagule supply with a constant based on the relative abundance of each species in the metacommunity.

We introduce niche differentiation during the replacement process by considering that propagules have to survive in the understory of adults prior to recruitment to adult size. Survival probability (λ_i) is a species-specific function of an environmental factor E (using a Gaussian function, such as in Tilman, 2004 – see Fig. 3.1):

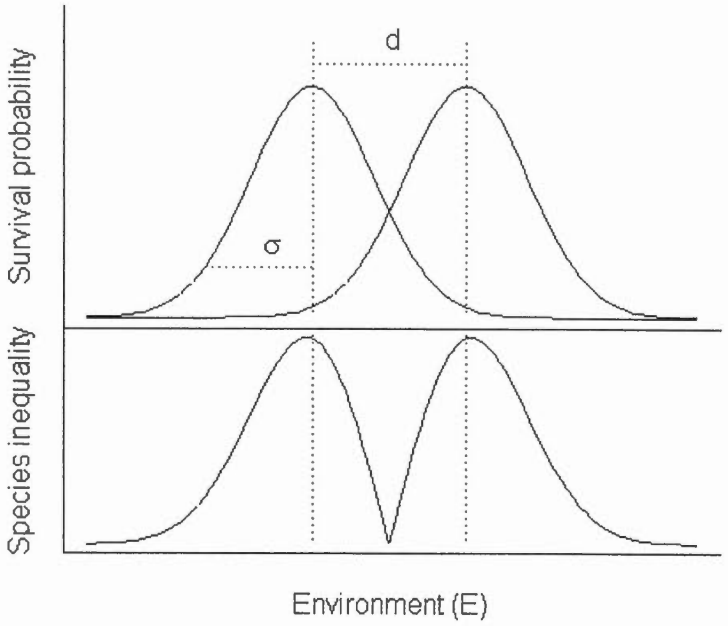
Eqn. 3. $$\lambda_i(E) = e^{\left[\frac{-(E-\mu_i)^2}{2\sigma^2}\right]}$$

where μ_i represents the optimal environmental condition for species i and σ is a parameter defining fundamental niche breadth. In this simple model (and ignoring dispersal limitation), the probability that a recruit will be of species i in a given environment is:

Eqn. 4. $$R_i = \frac{\lambda_i}{\sum_{j=1}^{s} \lambda_j}$$

In such a model, species inequality varies as a function of niche overlap (schematically illustrated on Fig. 3.1).

Figure 3.1 Schematic illustration of species fundamental differentiation along an environmental factor *E*. The fundamental niche overlap is inversely related to the distance between adjacent niches *d* divided by the fundamental niche breadth □. The species competitive inequality is given by the difference of survival probabilities between species at each value of the gradient *E*. Species are ecologically equivalent at a value of *E* where inequality is nil and their inequality increase with the distance for this "neutral" point. Species inequality declines with a decline in *d* or an increase in □.



When we combine these neutral and niche processes, the recruitment probability of species *i* at a given site is a function of the composition of the propagule supply at the replacement site and the specific survival rates (assuming independence of dispersal and survival). Then, with species equal for all traits except for survival as a function of E, the probability R_i of species *i* being recruited in a replacement event is:

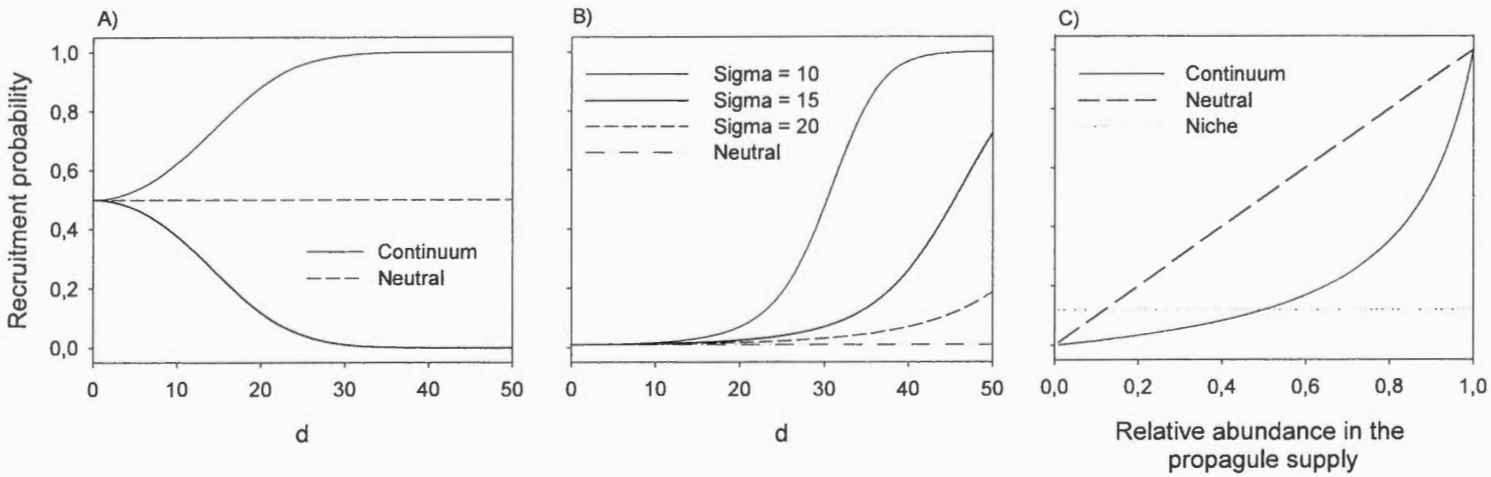
Eqn. 5.

$$R_i = \frac{\sum_{r=1}^{n} \lambda_i N_{i,r} W(r)}{\sum_{j=1}^{s} \sum_{r=1}^{n} \lambda_j N_{j,r} W(r)}$$

Equation 5 is a simple form of a spatially explicit recruitment model that takes into account both niche differentiation and neutral processes. Here, niche differentiation is based on interspecific differences in juvenile survival as a function of a single environmental axis (Eqn. 4). However, it could also have been based on differences in terms of growth, fecundity or germination, or even more complex mechanisms such as interactions with other trophic levels like animal dispersal in particular environmental patches, pest, herbivory and predation resistance. The neutral process in this model is dispersal limitation (Eqn. 2), because of the spatial distribution of the different populations of a community and their respective dispersal.

Before presenting the spatially-explicit simulations, we will first use three examples, based on the simple model described above, to illustrate how the relative importance of niche and neutral processes in Eqn. 5 can vary depending on competitive inequality (Eqn. 4) and species relative abundance in the propagule supply (Eqn. 2). These examples are necessary to explain the predictions further tested by simulations. The figures show the recruitment probability of a focal species in a two species competition during a single recruitment event, calculated from Eqn. 5. In all three examples, we assumed the environment (E) at the recruitment site to be homogeneous and the two species to be equal in all traits except for their optima (μ) (detailed parameters are given in the legend of Fig. 3.2).

Figure 3.2 Variation in recruitment probabilities for a two species community, following Eqn. 5. The environment in the replacement cell is fixed at a value of E = 50. A) The recruitment probabilities of two species with equal abundance in the propagule supply. The superior and the inferior competitors are respectively the upper and the lower solid lines. The dash line is the neutral prediction. θ = 10, θ_1= 50, θ_2= 50 – *distance between niches*; B) The recruitment probability of a superior competitor arriving as a singleton in the community increases as a function of distance between the niches, for different niche breadths. The dash line is the neutral model considering a community size of 100 individuals. θ_1= 50, θ_2= 50 – *distance between niches*; C) The recruitment probability of an inferior competitor as a function of its relative abundance in the propagule supply. The dotted line is predicted by the pure niche model of equation 4. The dash line is the neutral prediction. θ = 10, θ_1= 30, θ_2= 50.



The first example (Fig. 3.2a) illustrates a transition from stochastic to competitive exclusion as a function of species similarity. The figure depicts the recruitment probability of two species at equal abundances in the propagule supply, as a function of the distance between their niche optimums. The upper line corresponds to the species at its niche optimum and the lower line to the inferior competitor. The dashed line corresponds to the recruitment probability under a neutral model. The difference between the recruitment probabilities increases with the distance between the niches. Systematic competitive exclusion will be achieved with species having sufficient differences in their recruitment probabilities, as in the classical competition trials pioneered by Gause (1934) demonstrating competitive exclusion. However, according to the neutral model, further trials with equivalent species would have lead to a stochastic exclusion through a "random walk to extinction". As a consequence, the exclusion will be more deterministic as species differentiation increases.

In the second example (Fig. 3.2b), we show that extreme dispersal limitation can counteract competitive inequalities. In this example, the focal species is represented by a single propagule (invasion event) among a total input of 100 propagules, and has an optimum (μ) that corresponds to the prevailing environmental condition (E). A minimum distance between the niche optimums of the invader and resident species is necessary to counteract the resident species' advantage conferred by its higher relative abundance. This minimum distance varies depending on niche breadth. Without dispersal limitation, we would expect competitive exclusion to result in the species with the highest survival to exclude the other. However, the resident species has many more propagules than the invader, and thus has a demographic advantage even if it has lower survival. The more similar the two species are, the closer the recruitment probability is to the one of a neutral model (dashed line).

Finally, the third example (Fig. 3.2c) shows that variation in the relative abundance of species interacts with competitive inequalities to determine the recruitment probability. In this example, the focal species is the inferior competitor and its recruitment probability is given as a function of its relative abundance in the propagule supply. The neutral prediction is shown by the dashed line and the niche prediction without dispersal limitation is illustrated by the horizontal dotted line. Our continuum model (solid line) predicts the recruitment probability of an inferior competitor to be lower than that predicted by a pure niche model,

until the inferior competitor reaches a relative abundance of 0.5. After that threshold, the recruitment probability under the model combining niche differentiation and dispersal limitation is higher than the prediction under niche differentiation alone. Eventually, the inferior competitor reaches equal and even higher recruitment probabilities than the superior competitor.

3.4.2 Multi-species spatially-explicit simulations

It is not possible to extend the simple analytical model presented above to multi-species communities and a spatially-explicit environment. Therefore the following analyses rely on simulations. We used SORTIE-ND, an open-source software platform for spatially explicit simulation of forest dynamics (www.sortie-nd.org) to implement our model. Two life stages are considered in the model: adults and juveniles. The only processes included in the model are (1) adult mortality, (2) dispersal, (3) species-specific differences in juvenile survival as a function of environmental conditions and (4) recruitment from the juvenile to adult stage. The community is represented by a grid of 10,000 adults and is modelled as a torus to avoid edge effects. Each cell of the community grid can be occupied by only one adult. This grid is superimposed on a coarser scale grid that specifies environmental values for each adult cell: each cell of the environment grid is 5X5 adult cells in size. For simplicity, the environment is reduced to a single factor E, with conditions in each cell of the environment grid drawn randomly from a uniform distribution that ranges from 0 to 100. We assumed a uniform distribution to assure each species has the same probability of finding its optimal environment, and thus equivalent dispersal limitation. Unless otherwise noted, all runs use the same grid of environmental values.

At each time step, the model executes the routine summarized in Table 3.1. First, a fraction of the adult community is killed at random. All adult individuals are equal in their probability of death. We fixed the adult mortality rate at 25% per time step, comparable to values used in similar models (see Chave et al., 2002; McGill, 2003a). The mortality rate would not be expected to affect the predictions of a niche model unless species are differentiated by, for instance, lifespan and/or their responses to disturbance regimes (Loehle 2000).

The second step consists of the dispersal of juveniles by residual adults. Unfortunately, because computation time increases rapidly with the size of the community, we could not simulate an entire metacommunity. Instead, we simulated local community dynamics with a simplified treatment of dispersal from the surrounding metacommunity, as in previous neutral models (Bell, 2000; Hubbell, 2001; Chave et al., 2002). Dispersal within the simulated community was modelled with a continuous dispersal kernel as suggested above. The probability of a juvenile reaching a cell located at a distance r from an adult parent of the local community is modelled with the following kernel:

Eqn. 6.
$$W(r) = e^{-wr^2}$$

where w determines the shape of the dispersal kernel. The value of w was chosen to produce a default median dispersal distance of 5 adult cells, which by analogy is approximately 25 meters in a forest with trees of 5 meters crown diameter. The parameter m in Eqn. 1 gives the proportion of juveniles from all species that reached the local community via non-spatially explicit immigration. The metacommunity was assumed to be constant in composition and species relative abundance was assumed to follow a log-series distribution. Preliminary trials showed the results to be the same with a uniform distribution of species in the metacommunity. Bell (2000) assumed a stationary uniform distribution of species abundances in the regional species pool and found results consistent with Hubbell (2001). Thus, each species has a probability of immigration scaled to its abundance in the metacommunity. Fecundity is equal for all species and was determined from preliminary trials so that the combined input from local and long distance sources would produce approximately 10 to 20 juveniles per adult. By comparison, this corresponds roughly to sapling density in temperate forests (Pacala et al., 1996). Results from preliminary simulations were not sensitive to fecundity, and therefore we do not discuss it further.

Niche differentiation occurs in the third step (Table 3.1) through variation among species in juvenile survival as a function of the environmental condition within the grid cell (Eqn. 3; Fig. 3.1). Each species has a unique niche optimum (μ_i), and the niches are regularly spaced along the environmental axis. The distance between adjacent niche optima

corresponds to the range of E (100) divided by the number of species. Unless otherwise specified, niche breadth (σ) was set at 10 and was equal for all species.

Finally, when an adult dies, it is replaced by a juvenile picked at random from those located in the adult cell. Juveniles stay in the understory of adults until they are recruited or die. Thus, the recruitment probability for species i in a given adult cell is equal to the relative abundance of that species among the juveniles in the cell. Preliminary testing confirmed that this model produces competitive exclusion when niche differences are sufficient, while it creates a random drift when species are ecologically equivalent.

3.4.3 Simulation scenarios and data analysis

The first set of simulations was a gradient of species richness from 5 to 100 species. Two different scenarios were used. In the first, a constant niche overlap (i.e. distance between niches/niche breadth = 1) was maintained as species richness increased through a decrease in niche breadth. This allowed us to test the effect of increasing dispersal limitation with increasing species richness, without the effect of increasing niche overlap. In the second scenario, we held niche breadth constant ($\sigma = 10$) to test the effect of increasing niche overlap with increasing species richness.

The second set of simulations tests the consequences of increasing niche overlap (through an increase in niche breadth from 1 to 50) in a community of 10 species. The third set of simulations tests the consequences of increasing dispersal capabilities. We varied the dispersal parameter w to produce a gradient of median dispersal distance from 5 to 50 meters in a community of 10 species. The above simulations did not include immigration to track the neutral drift. For these simulations, all runs start with 25 saplings of each species per adult cell. By doing so, a fast selection of the top competitor occurred for each site at the beginning of the run and thus prevents dispersal limitation at the initiation of the simulation.

A community solely driven by competition will have a deterministic succession, while a neutral community will have the maximum stochasticity among replicated successions because of the neutral drift (Clark and McLachlan, 2003). We used this proxy to assess "neutrality" when we tested the different predictions presented above. For each of the three

sets of simulations described above, we repeated the simulations with all species having the same niche optimum. This serves as a "neutral control". We then calculated a "neutrality index" by dividing the variance in species abundance among replicated runs under a given scenario (differentiated species) by the variance among replicates for the "neutral control" (undifferentiated species). The index ranges from 0 to 1, with 0 being absolutely deterministic (niche) and 1 being completely stochastic (neutral). The variance was calculated for each species among 50 replicated runs and then averaged for the whole community. The index was calculated after 500 time steps. This is not a sufficient run length to reach a truly stable species composition, but preliminary simulations showed that index differences among scenarios were similar when the run length was longer than 500 time steps.

We compared the abundance distribution of species with different levels of immigration. We simulated communities in which none, 10^{-3} and 10^{-1} of the new juveniles each time step were immigrants. The metacommunity consisted of 149 differentiated species with their optima drawn at random (distance between niches = 0.67, and niche breadth σ = 10). Simulations were run until composition stabilized (5 000 and 20 000 time steps respectively with and without immigration). Species arrive in an initially bare community following immigration events, except for the scenario without immigration where we started the community with the set of 149 species. For comparison with Tilman (2004), a scenario with a fraction of 10^{-1} immigrants and a Gaussian frequency distribution of environmental conditions was also simulated. Species were ordered by their niche optimum and their abundance plotted to visually examine the abundance against the distance between niches for the different scenarios.

Table 3.1 Summary of the model simulation routine and corresponding parameters.

Step	Event	Parameters
1	Adult random mortality	Mortality rate (non specific)
2	Dispersal	Dispersal w (non specific) Immigration m (specific)
3	Juvenile survival	Niche mode μ (specific) Fundamental niche breadth σ (non specific) Grid of E values (independent of species occurrence)
4	Juvenile recruitment	-

3.5 Simulation results

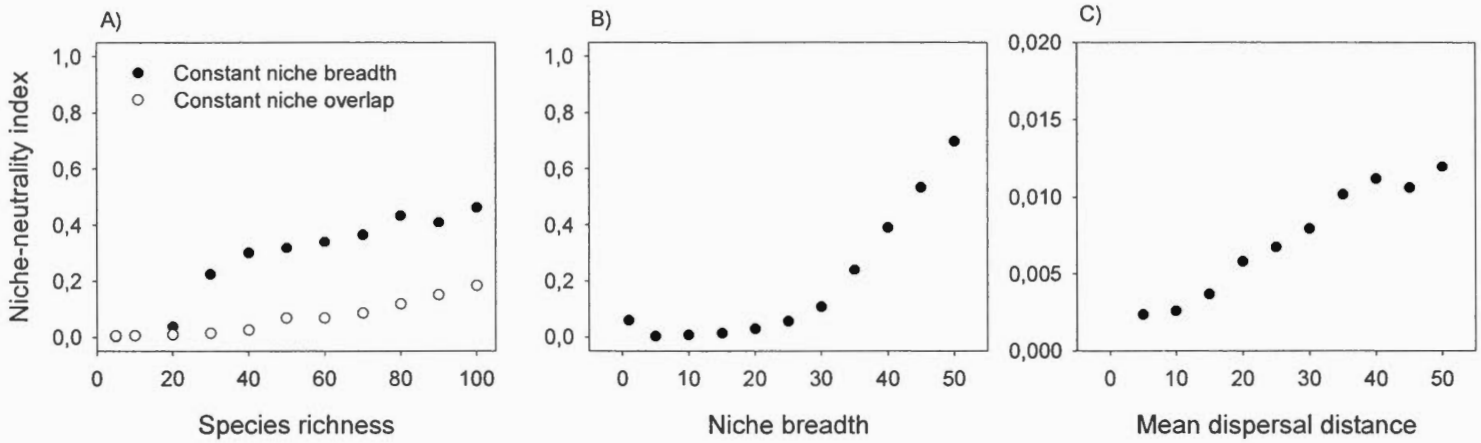
3.5.1 Species richness and niche overlap

Increasing species richness resulted in increasing neutrality, whether niche overlap was kept constant or increased (Fig. 3.3a). Increasing species richness increases the potential for dispersal limitation (i.e. lack of propagules to colonize suitable sites) and thus promotes neutrality. We did not observe a pattern of "realized partitioning" in the high species richness scenarios (Tilman, 2004; Schwilk and Ackerly, 2005). In principle, species could have colonized the most favourable sites, reduced their realized niche breadth and maintained their dominance on these sites, but we did not observe this in the simulations. There was also a clear relationship between niche breadth and neutrality in the set of simulations with increasing species fundamental niche breadth (Fig. 3.3b). In those simulations, dispersal limitation was low and constant among scenarios. Again a realized partitioning of the environment could have occurred despite increasing fundamental niche breadth, but it was not observed in the simulations.

3.5.2 Local dispersal

Neutrality increased as local dispersal distances increased, as predicted (Fig. 3.3c). However, the effect was much less pronounced than what was observed when species richness and niche overlap were increased (Fig. 3.3a,b). It is possible that the range of the stochasticity gradient could have been affected by the arbitrary choice of the grain size of the environment. For these simulations, the environment was simulated as a grid of cells holding 25 adults. We performed simulations with different grain sizes (not shown) and found that neutrality is inversely related to grain size. Under the assumption of spatial heterogeneity fixed in time, the likelihood that a propagule falling from an adult already located on a favourable site lands on a favourable site depends on the dispersal capabilities relative to the grain size of the environment. Thus, the capacity of a superior competitor to maintain its occupancy of a suitable site, against successful stochastic recruitment of inferior competitors, is inversely related to the ratio of the dispersal capabilities over the grain size.

Figure 3.3 Gradient from niche to neutrality as a function of A) species richness with constant niche breadth (= 10) and constant niche overlap (d/ = 1); B) niche breadth; C) median dispersal gradient. Environmental values *E* range from 0 to 100, each species has a unique niche and a cell of the environmental grid is 5X5 adults in size. Unless specified by the scenario, default niche breadth = 10, median dispersal distance = 5 adults, species richness = 10 species. There is no immigration in these simulations. The index ranges between 0 (niche) and 1 (neutral).



3.5.3 Immigration

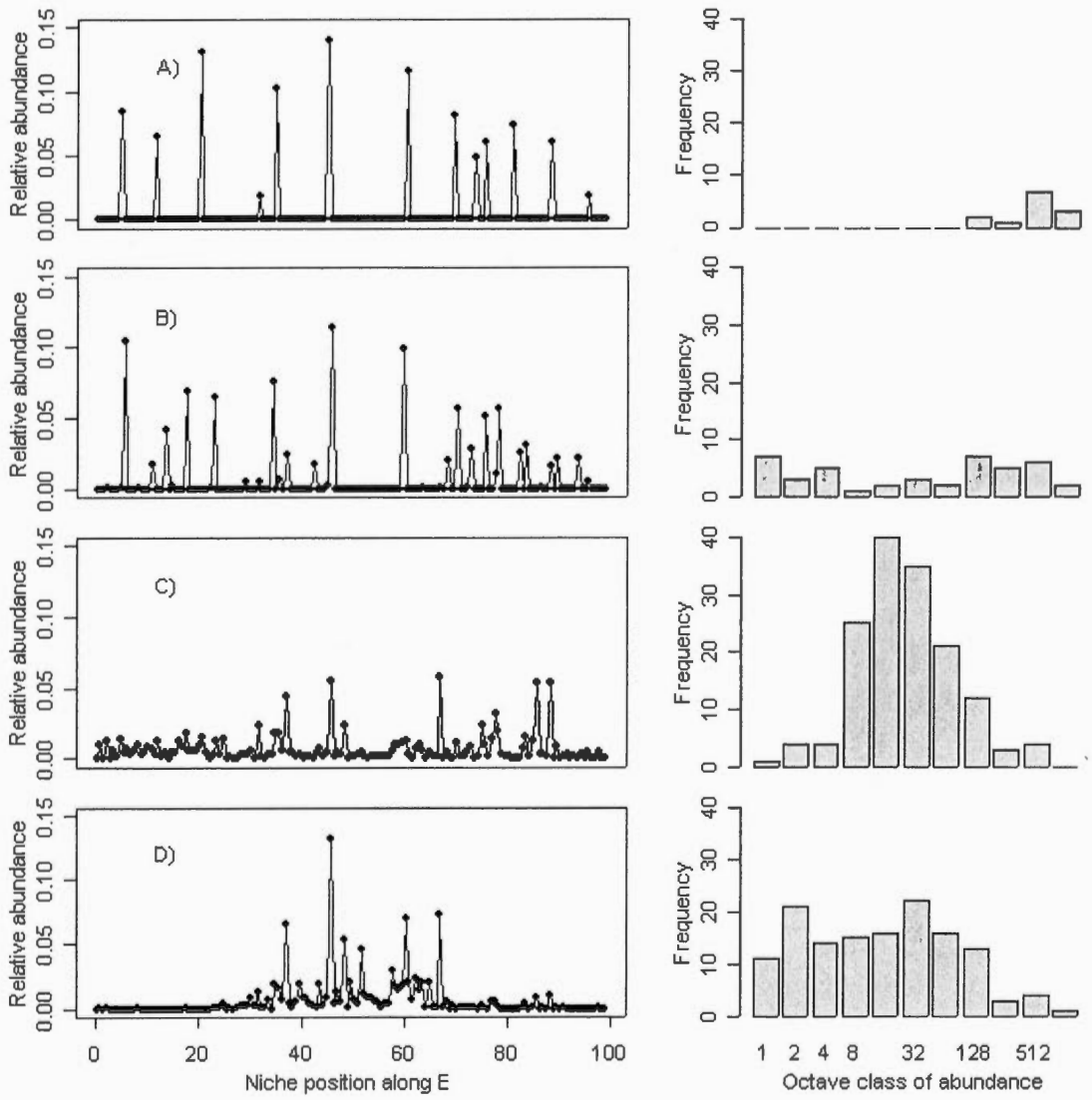
Simulation with no immigration (i.e. local dispersal only) produced communities of low diversity (13 species out of a regional pool of 149), and regular spacing between the dominant species' niche optima (i.e. clear limiting similarities) (Fig. 3.4a). Increasing amounts of immigration resulted in increasing numbers of rare species in the community (Fig. 3.4b and 3.4c), as predicted by neutral models (Bell, 2000; Hubbell, 2001). At a low immigration level (Fig. 3.4b – 43 species), the rare species were located between the dominant species, which were still more or less regularly spaced. Thus, at low immigration rates, the pattern of relative abundance of species within a community will be strongly influenced by the distribution of environmental conditions. The specific identity of the winners in the successional contest will be the result of the sequence of invasion events at the beginning of the succession, since the first species to arrive at a site can limit the success of the subsequent immigrants by stochastic exclusion (Tilman, 2004). As the amount of immigration increases, the community structure will be increasingly affected by stochastic exclusion (Fig. 3.4c – 149 species). At high immigration rates, there will be a high degree of niche overlap and similar species will be subject to neutral dynamics.

The last simulations revealed an important interaction between environmental heterogeneity and immigration from a metacommunity (Fig. 3.4d). A change in the frequency distribution of the environmental conditions can have a considerable impact on the relative abundance distribution of species, even with a relatively high amount of immigration. Under the assumption of a Gaussian frequency distribution of environmental conditions (Fig. 3.4d), the frequency of rare species is considerably higher than under a uniform distribution of environmental conditions (Fig. 3.4c). These rare species are more dispersal limited and thus subject to drift, but they are sustained by immigration (under a form of source-sink dynamics) and successfully reintroduced after local extinction.

3.6 Discussion

Our analyses suggest three general conclusions. First, competiton and stochastic exclusion can both simultaneously drive community dynamics and structure species

Figure 3.4 Species abundance distributions at different immigration intensities. A) m = 0; B) m = 0.001; C) m = 0.10 ; D) m = 0.10, but the distribution of environmental values E follows a Gaussian distribution. On the left side of the figure, the species are ordered by the rank of their niche optimum along the gradient of E. On the right side are the corresponding frequency distributions of species abundance by octave class of abundance (sensu Preston 1948). Default parameters are the same as in Fig. 3.3.



assemblage. The relative importance of competitive versus stochastic exclusion creates a continuum from niche-structured communities to neutral structure. Secondly, joint effects of competition and dispersal are sufficient to create this continuum. Competitive inequality between species determines the extent to which demographic limitations in the propagule supply will affect community dynamics. In turn, demographic limitations are created by the interplay of the spatial configuration of the community with the dispersal capabilities at both local and long distance. Ultimately, the pattern of relative abundance of species within a community results from the balance between competitive and stochastic exclusion. In relatively isolated communities, immigration from metacommunities is insufficient to balance the exclusion processes, diversity is low, and niche differentiation is ultimately the dominant process affecting species abundances. The species tend to have non-overlapping niches, and their relative abundance depends on the distribution of environmental conditions. Rare species will be maintained with increasing immigration. Thus, high immigration prevents the establishment of a limit to similarity and increases species richness. In such conditions, niche overlap is high and community dynamics is dominated by stochastic exclusion.

Numerous studies have incorporated stochasticity in models of recruitment, following the work of Hurtt and Pacala (1995). Among them, Tilman (2004) has proposed a stochastic niche theory as a revision of classical competition theory (Tilman, 1982). The stochastic niche theory predicts patterns of species relative abundance that are similar to those predicted by the neutral model. In Tilman's (2004) model, the structure of abundance of a community results from the interplay of the frequency distribution of environmental conditions and specific traits of the invaders (Tilman 2004). The establishment of a stochastic limit to similarity prevents infinite diversity. Thus, the diversity of a community under this model depends on the capacities of the species to partition the environmental gradient. However, Tilman (2004) did not take into account the impact that various intensities of immigration and dispersal limitation could have on the predicted outcome. The results presented here clearly demonstrated these are factors that can counterbalance niche differentiation. Therefore, we argue the stochastic niche theory is not a complete reconciliation between niche and neutrality.

Under neutral models, the shape of the relative abundance distribution results from the balance between stochastic exclusion and the supply of new species (Bell, 2000; Hubbell, 2001). Some models that also include niche differentiation (Chave et al., 2002; Purves and Pacala, 2005) can produce similar relative abundance patterns, as long as species richness is kept elevated through substantial immigration or speciation. It has been argued that observing patterns of species abundance typically predicted by neutral models can not necessarily be taken as evidence of neutral processes (Purves and Pacala, 2005), and our results concur with that. However, our results also show that the observed patterns can result from a neutral drift created by an elevated niche overlap, sustained by the constant reintroduction of excluded species through high immigration and/or speciation rates. Under such conditions, the rare species are transients and their occurrence depends on immigration; on the other hand, the resident species are permanent and their occurrence depend on niche differentiation (Magurran and Henderson, 2003; Schwilk and Ackerly, 2005).

A model of community dynamics that unifies recent theoretical developments to predict patterns of species abundance should combine the dispersal limitation component of the neutral models and the stochastic niche concept pioneered by Tilman (2004). The model we proposed incorporates these two concepts in a manner that unifies these perspectives. According to our model, diversity patterns are the consequence of the balance between stochastic and competitive exclusion. In the absence of immigration and speciation, species differentiation tends to create a regular spacing of niches along an environmental gradient, as would be predicted by the stochastic niche model of Tilman (2004). These species are complementary because they do not compete intensively with each other. Their abundance is dictated by the frequency distribution of environmental conditions. Between these complementary species, immigration and speciation will introduce to the community species that are similar to the complementary species. Because these species are redundant to some of the resident species, they will tend to be excluded both by competition and random drift. By chance, in some rare events, they could replace the dominant species after a random drift. The importance of immigration will determine the amount of redundancy, and as a consequence, the balance between stochastic and competitive exclusion in structuring communities. Ultimately, we expect the species richness and diversity structure of a community to be a

function of the frequency distribution of environmental conditions, community isolation (because of dispersal limitation, species turnover rate and spatial distribution of resources) and speciation processes (in intensity and diversity of species traits).

3.7 Conclusion

One of the most important innovations of neutral models has been to explicitly link local community dynamics to metacommunity dynamics. In this study, we used a simplified representation of this interaction by assuming that the distribution of species relative abundance in the metacommunity corresponded to a stationary log-series. Essentially, we incorporated the metacommunity using a mass-effect perspective (Leibold et al., 2004), where the metacommunity is a source of immigrants that can potentially rescue extinct species and introduce new species in the local community. However, in reality, metacommunities are obviously dynamic. Under the neutral model, speciation is a necessary process to balance the extinction of species at the regional scale (Hubbell, 2001). Speciation also creates innovation in species traits, which can impact community dynamics under a niche perspective (Tilman, 2004). Combined with dispersal limitation, speciation is responsible for spatial patterns in species distribution. The mass-effect is possible when such regional spatial patterns occur (Mouquet and Loreau, 2002). Thus, we agree that local dynamics can be affected by the speciation process at the regional scale. For instance, a non-stationary metacommunity could introduce a greater amount of variability in the identity of the redundant species, and occasionally replace the complementary species. However, we do not expect that a dynamic metacommunity would change the essence of our results, since the mass-effect perspective of the metacommunity would still remain. Nonetheless, we recognize more work is needed to assess the generality of the continuum hypothesis at the scale of the metacommunity.

Perhaps one of the most interesting results of our model is increasing neutrality with increasing species richness. Careful attention must be paid to this prediction. We emphasize that the mechanism generating this prediction is the presumption of increasing niche overlap with increasing species richness. However, we could expect some communities to be species rich and niche-dominated, because of a highly heterogeneous environments that enables low niche overlap, just as we could expect some species-poor communities to be neutral because

of a homogeneous environment that increase niche overlap. In general, our prediction is that ecological drift will increase with species richness once a community becomes saturated with complementary species and immigration maintains the presence of redundant species.

There is considerable indirect empirical support in the literature for the continuum hypothesis we have presented here. We have argued that the interaction between niche overlap and dispersal limitation is an essential feature for the continuum from niche to neutrality. As Hubbell (2001) has pointed out, the contrast between temperate and tropical forests dynamics offers a clear example of this continuum. There is a well known trade-off between high-light growth and low-light survivorship in temperate forest (Kobe et al., 1995). Shade tolerance is thus a successful predictor of species abundance ranking along a successional sequence (Pacala et al., 1996). The predictability of species ranking is much less clear for tropical forests, where important overlap occurs along this trade-off axis (Hubbell, 2001), and where species composition in gaps is more reflective of neighbourhood composition (Hubbell et al., 1999). However, more direct support for the hypothesis is clearly needed. Among others, one prediction made in our study was that the ecological drift in a succession increases with increasing niche overlap, and thus presumably with species diversity. One could test this by measuring the variability in succession of a two factor experiment controlling simultaneously for species richness and immigration (in grasslands for instance). The long term monitoring of diversity/ecosystem functioning experiments such as BIODEPTH (Loreau and Hector, 2001) thus offer a great opportunity for testing one of the main prediction presented here.

CHAPITRE IV

LIMITS TO THE QUANTIFICATION OF NICHE DIFFERENTIATION AND DISPERSAL LIMITATIONS WITH CANONICAL ORDINATIONS

Dominique Gravel et Tim Work

4.1 Résumé

La dispersion limitée et les interactions compétitives sont d'importants facteurs qui structurent les communautés. Parce que les communautés sont vraisemblablement situées à quelque part entre les extrêmes de la dynamique neutre et des interactions compétitives pures, il est pertinent de pouvoir quantifier la contribution relative des deux types de processus dans le façonnage de la distribution des espèces. Il y a un engouement récent pour l'utilisation du cadre méthodologique de partition de la variance de données multivariées de Borcard et al. (1992) pour tester la théorie neutre, sa supposition sous-jacente d'équivalence écologique et quantifier l'importance de la dispersion limitée. L'objectif principal de cette étude est de souligner d'importantes limites à cette approche. Nous sommes inquiets qu'une large part de la variance inexpliquée souvent rencontrée dans ces études est le résultat de l'usage de modèles inadéquats pour tester les hypothèses. Notre premier argument est que les techniques d'ordination multivariées ne sont pas adéquates pour tester l'hypothèse de différentiation des niches. Notre second argument est que, même si la structure spatiale des communautés peut résulter de la dispersion limitée, sa quantification est un test faible de la neutralité, basé sur la description de patrons plutôt que sur le test d'hypothèse. De surcroît, il sera montré que la dispersion limitée dans un environnement spatialement hétérogène peut conduire à une sous- ou une sur-estimation de la réponse des espèces à l'environnement dans le contexte traditionnel des analyses multivariées. L'argumentation est basée sur l'analyse de deux jeux de donnés simulés et d'un jeux de données récoltées sur le terrain, sur la distribution spatiale de gaulis dans une forêt tempérée du nord-est américain. Nous concluons que des approches plus mécanistiques, au détriment des approches d'évaluation de patrons, sont nécessaires pour distinguer la contribution relative de la dispersion limitée et des interactions compétitives sur la distribution des espèces.

Mots-clés : Différentiation des niches, dispersion limitée, théorie neutre, analyse canonique des correspondances

4.2 Abstract

Dispersal limitations and competitive interactions are important factors structuring communities. Because real ecological communities likely lie between the extremes of neutral dynamics and pure competitive interactions, it is relevant to quantify the relative contribution of both types of processes in the shaping of species distribution. There is a recent interest in the use of the multivariate partitioning framework proposed by Borcard et al. (1992) to test neutral theory, its underlying assumption and a quantification of dispersal limitations. The primary purpose of this study is to highlight important limitations of this approach. We are concerned that the high fraction of unexplained variance commonly seen in studies using this methodology results from having inadequate modelling tools to test the corresponding hypotheses. Our first argument is that multivariate ordination techniques are not adequate methods to test for niche differentiation. Our second argument is that, although the community spatial structure could result from dispersal limitations, its quantification is a weak test of neutrality based on pattern description rather than hypothesis testing. Moreover, it will be shown that dispersal limitations in a spatially heterogeneous environment could lead to both under- and over-estimation of species response to the environment with the traditional multivariate framework. The argumentation is based on the analysis of two simulated datasets and one field dataset on saplings spatial distribution in a deciduous temperate forest. We conclude that more mechanistic approaches, rather than curve fitting exercises, are required to partition the contribution of dispersal limitations and competitive interactions in the species distribution.

4.3 Introduction

It is now widely recognized that spatial processes such as dispersal limitation (Tilman, 1994; Hurtt and Pacala, 1995; Hubbell, 2001; Mouquet and Loreau, 2003; Gravel et al., 2006) and competitive interactions (Bolker and Pacala, 1997) are important factors structuring communities. At the one extreme, there is a neutral dynamic, where the spatial structure of a community results from a balance between random extinctions and the introduction of new species through immigration (or speciation at the regional scale, Hubbell [2001]). Dispersal limitations slow diffusion of species across landscapes and prevent homogenization of the local community. At the other extreme, in the absence of dispersal limitations, the dynamics and the structure of the community have been attributed to competitive interactions. Because real ecological communities likely lie between these two extremes (Gravel et al., 2006), it is relevant to quantify the relative contribution of both types of processes in the shaping of species distribution.

The multivariate variance partitioning framework originally proposed by Borcard et al. (1992) and further developed by Bocard and Legendre (2002) has been widely advocated to quantify the relative importance of environmental variables and spatial structure in modelling species distribution. This framework was originally proposed to model species distribution as a function of environmental variables, taking into account the spatial autocorrelation of species distribution (Leduc et al., 1992; Borcard et al., 1992; Legendre, 1993). It is only recently that this methodology has been widely used as a test of the neutral theory, its underlying assumption and a quantification of dispersal limitations (e.g. Svenning et al., 2004; Hardy and Sonké, 2004; Gilbert and Lechowicz, 2004; Karst et al., 2005). It has also been used to differentiate among different perspectives on metacommunity dynamics (Cottenie, 2005). These tests basically assume the fraction of variance explained by environmental variables is a measure of niche differentiation, while the spatial structure is a measure of dispersal limitations.

The primary purpose of this study is to highlight important limitations of this approach to quantify the relative importance of niche differentiation and dispersal limitations. We are concerned that the large fraction of unexplained variance commonly seen in studies using this methodology, somewhere between 30 to 80% (see for instance the meta-analysis of Cottenie

[2005] on 158 datasets), has been interpreted in terms of community dynamics instead of other alternative, plausible hypotheses. This unexplained variance can arise from sampling error, demographic stochasticity, but can also result from an inadequate model to test for niche and neutral processes. Our first argument is that multivariate ordination techniques are not adequate methods to model niche differentiation. We will show a strong limitation of these techniques going against the niche theory. Our second argument is that, although the community spatial structure could result from dispersal limitations, its quantification is a weak test of neutrality (McGill, 2003), based on pattern description rather than hypothesis testing. Moreover, it will be shown that niche differentiation in a spatially heterogeneous environment could lead to both under- and over-estimation of dispersal limitations with the traditional multivariate framework. These arguments are based on the analysis of a simulated community with perfect niche differentiation along an environmental gradient, the second analysis is based on results from stochastic spatially explicit simulations and the third dataset consists of field data on the spatial distribution of two forest tree species regeneration in a mature deciduous forest of northeastern America.

4.4 Niche differentiation along an environmental gradient

Multivariate methods of variance partitioning may not be efficient to model niche differentiation. Such methods result in a large fraction of unexplained variance that is partly attributable to the incapacity of the model to catch the species niche differentiation. To show this, we simulated a deterministic and perfect community turnover along a single environmental gradient. Four scenarios were simulated, corresponding to a gradient of niche overlap (distance between modes (d)/ niche breadth (□) = 2, 1, 0.5, 0.1). Each scenario consists of 100 sites representing a gradient of E from 1 to 100. This vector was used as the environmental matrix in the multivariate analyses. For each of the 25 species simulated, the abundance is a deterministic gaussian-shaped function and the modes are regularly spaced along the gradient. The niche breadth is the same for every species, and given the above scenarios, are respectively 2, 4, 20 and 40. These conditions meet the same unimodal species response model criteria cited by Ter Braak (1985) which form the analytical base of commonly used multivariate methods which partition variation such as Canonical Correspondance Analysis.

Species abundance was modelled with the Canonical Correspondance Analysis (Legendre and Legendre, 1998) and the Redundancy Analysis (RDA) performed on Chord, Chi-square and Hellinger transformed abundances (Legendre and Gallagher, 2001). Because the simulated species abundances are deterministic, we should expect 100% of the variance to be explained, regardless of the amount of niche overlap.

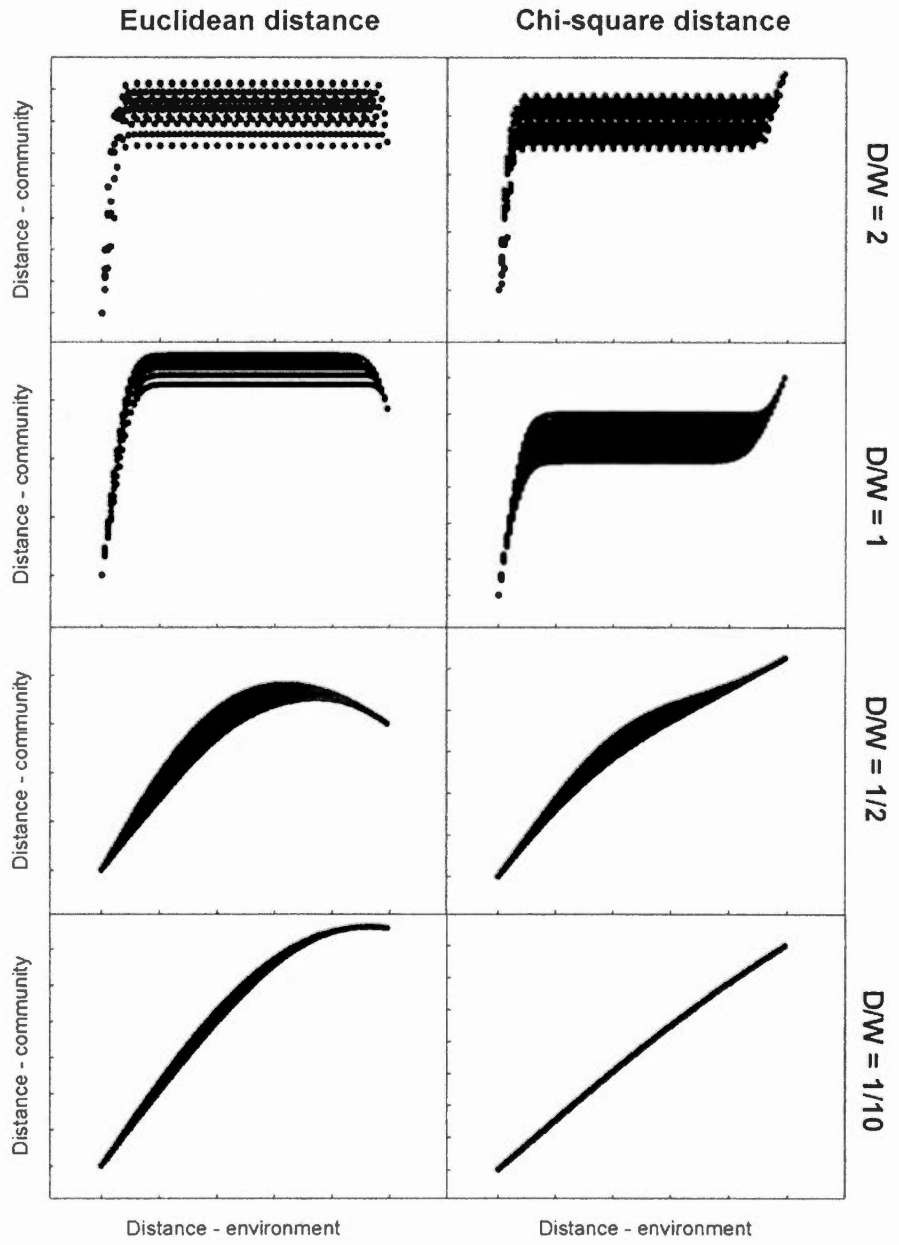
The fit of the different models to the data varies highly with the amount of niche overlap (Table 4.1). For all methods, the amount of variance explained increases with the level of niche overlap. The four methods performed poorly at levels of overlap of 2 and 1. This is relevant as niche theory predicts stable coexistence for levels of niche overlap larger than 1 (MacArthur and Levins, 1967). The methods therefore performed the worst where niche differentiation is strongest. Variability among methods is negligible in comparison to variability among levels of overlap; the best method however is the RDA on Hellinger-transformed species abundance.

Ordinations with the RDA and the CCA are respectively Euclidean and Chi-square - based methods (Legendre and Legendre, 1998). Transformation of species abundance data could make the RDA to respect other distance metrics such as the Hellinger, the Chord and the Chi-square metrics (Legendre and Gallager, 2001). The relatively poor performance of the various multivariate methods performed here to capture the species structure into the data results from the levelling off of the distance metric after a threshold environmental distance along the gradient (Figure 4.1). Whatever the distance metric used, the distance between two communities peaks after a complete species turnover. After this threshold, the distance metric between two communities will be constant, no matter if the environmental distance is small or large. Because the amount of niche overlap determines species turnover rate along the environmental gradient, it will affect the shape of the relationship between the environmental distance and the community distance.

Table 4.1 Performance of different multivariate methods to test for the niche differentiation in the deterministic simulation dataset.

Method	Niche overlap	Total inertia	First axis eigenvalue	Variance explained (%)
CCA	2	13.4263	0.9952	7.4
	1	6.4464	0.9807	15.2
	0.5	0.8150	0.5963	73.2
	0.1	0.1649	0.1584	96.0
RDA - Chord transformation	2	0.9391	0.0683	7.3
	1	0.8724	0.1261	14.5
	0.5	0.4329	0.2912	67.3
	0.1	0.1358	0.1269	93.4
RDA - Chi2 transformation	2	13.6930	1.0340	7.6
	1	6.7200	1.0500	15.6
	0.5	0.9324	0.6893	73.9
	0.1	0.1876	0.1803	96.1
RDA - Hellinger transformation	2	0.9117	0.0927	10.2
	1	0.8188	0.1680	20.5
	0.5	0.2761	0.2296	83.2
	0.1	0.0500	0.0489	97.9

Figure 4.1 Relationship between the environmental distance (euclidean) and the community distance (Euclidean and Chi-square) for different levels of niche overlap in the deterministic dataset (D/W, D: distance between adjacent niches, W: niche breadth).



The levelling of the distance metric results in a strong arch effect as indicated by the numerous positive eigenvalues on non-canonical axes. Given that only one environmental axis is structuring our simulated communities, the right model should result in a single ordination axis whatever is the amount of niche overlap. However, there are almost as many positive eigenvalues as there are species, all of which contribute almost equally to the model. This effect arises as a necessary geometric property of distances between sites and species. To illustrate this point, let us consider the sites A, B and C along a single hypothetical environmental gradient and assume there are no species in common between the sites. If A and C are a two extremes of the gradient and B in the middle, even if in reality there is only one gradient, the only way to ordinate sites with respect to the distance between them sites is to have two ordination axis (A, B, and C will be represented as a triangle in the ordination space). As a result, the strongest will be the species turnover along the environmental gradient (because of niche differentiation), the more ordination axes will be necessary and the stronger will be the arch effect.

4.5 Stochastic spatially explicit simulations

Now turning to the analysis of spatial patterns in species distribution, it is relevant to ask if the traditional methods, using either a polynomial or PCNM variables to perform a trend surface analysis, are adequate descriptors of dispersal limitations. It was argued in the introduction these methods do not allow testing the hypothesis of dispersal limitation, only for modelling species spatial distribution. Here, we used an individual-based and stochastic simulation model to generate a spatially explicit distribution for 25 species. Since we know the parameters at the origin of the dataset, it facilitates the comparison of different methods to adequately model species distribution.

The model simulates a heterogeneous environment on which species are differentiated by their juvenile survival (see Gravel et al. [2006] for a complete description of the model). The community is represented by a 100*100 lattice (analysis are conducted on a subplot of 30*30), for which each cell is filled by an adult and has an independent environmental condition E. After the death of an adult, recruitment is a lottery function among understory juveniles, analogous to canopy recruitment in a forest after a treefall gap. Abundance of juveniles in a given cell depends on two processes: first the quantity of juveniles reaching the

cell through local dispersal and immigration (neutral part of the model) and juvenile survival at this particular environmental condition (niche part of the model). The average dispersal distance of the simulated Weibull kernel is five cells. The fraction of immigrants in the seed rain at carrying capacity is 0.001 (a uniform distribution in the metacommunity is assumed for simplicity). The environmental optima of the 25 species are regularly spaced along the gradient of E, ranging from 0 to 100, and the niche breadth (survival is a gaussian-shapped function) is 25. Adults death rate is 1%. No species is present at initiation and the community develops after successive species immigration. The simulation lasts 5000 time-steps.

The dynamics of the simulation model is driven by recruitment probabilities, i.-e. juvenile distribution. Thus, the analysis is devoted to this stage. It closely matches the analysis of understory sapling composition in a mature forest. Four different analyses were performed to assess the importance of spatial and environmental variables to explain species distribution. First, juvenile distribution was modelled following the method of Borcard et al. (1992), using the third degree polynomial of the X and Y coordinates and the environmental condition E as explanatory variables. Second, juvenile distribution was modelled using the PCNM methodology of Borcard and Legendre (2002). This method performs a spectral decomposition of the spatial pattern. Only the first 100 PCNM variables were used and a forward selection procedure with a stopping criteria of p = 0.1 was used prior to perform the variance partitioning. Third, we calculated for each cell the expected composition of the seed rain, given the dispersal kernel and the neighbourhood composition of the adult community. The matrix of the expected seed rain for every species is later used as the spatial predictor of juvenile distribution. We expected this approach to be the adequate quantification of dispersal limitation. Fourth, given the above results with the deterministic dataset of niche differentiation, rather than using a multi-species approach, we modelled each species distribution individually by non-linear least-squares. The niche model of species *i* abundance (A) is $A_i = \kappa_i \lambda_i(E)$, where $\lambda_i(E)$ is the species response to the environment and κ_i is the species abundance at optimum. In this case, species response to the environment is $\lambda_i(E) = \exp\left[\frac{-(E-u_i)^2}{2\sigma^2}\right]$, where u is the optimum and σ is the niche breadth. The neutral

model is $A_i = \alpha_i \sum_{r=1}^{n} N_{i,r} W(r)$, where $N_{i,r}$ is the number of adults of species *i* at distance *r*, W(r) is the dispersal kernel and □ is a scaling constant. Finally, the mixed model is $A_i = \alpha_i \lambda_i(E) \sum_{r=1}^{n} N_{i,r} W(r)$. This model almost exactly reproduces the simulation model, where the abundance of juveniles is a function of the survival of incoming seeds, and thus will provide us a good comparison to other methods. For the analysis one to three, we used RDA on Hellinger-transformed species abundance to partition variation among environmental and spatial variables (the method that performed best in the above analysis of deterministic niche differentiation). Note however for the fourth analysis, the model is not linear, and thus it is not possible to partition the variance.

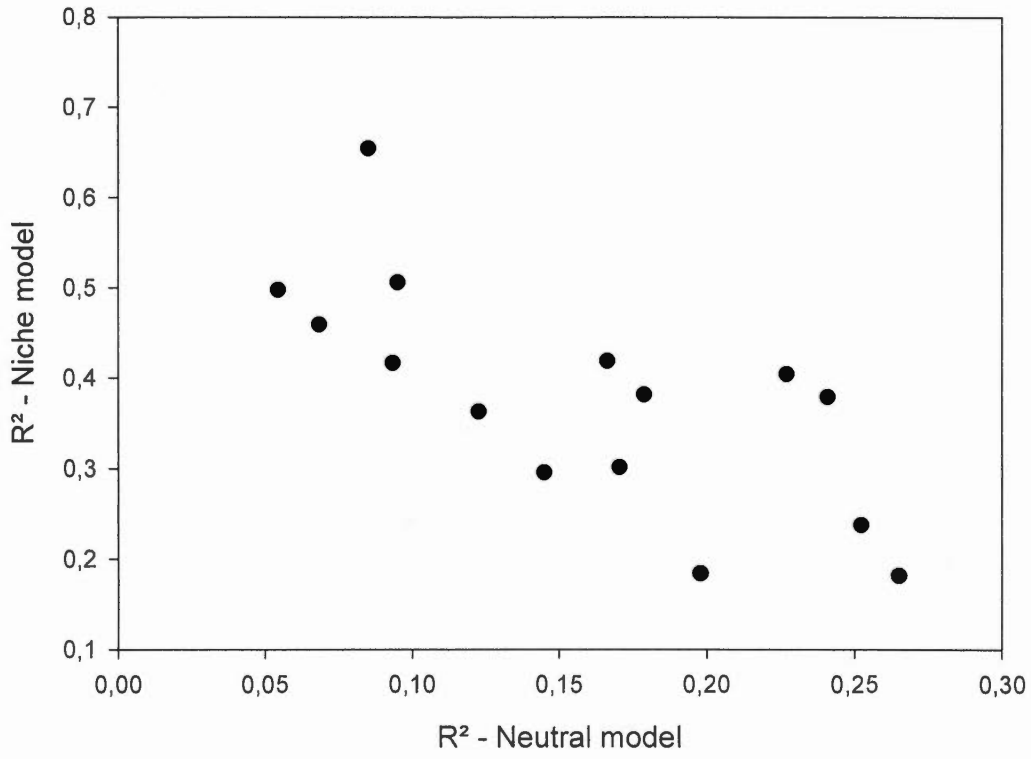
The comparison of the different methods is presented at Table 4.2. All variables performed similarly to catch the spatial structure of species distribution. The fraction of variance explained by the spatial variables ranges between 12.5% for the polynomial to 15.7% for the average of the species specific models (minimum and maximum of 5.4 and 26.5%). The expected seed rain is therefore, at least, an equal predictor of species spatial distribution to the traditional method. Not surprisingly, given the absence of spatial structure in the environment, the fraction [b] representing the joint information between spatial and environmental variables is extremely low. All three multivariate methods performed similarly to model species relationship with the environment. In agreement with the results from the above section, the species specific models performed however much better to model species distribution as a function of the environment.

The most interesting result from this exercise is the synergistic effect of combining dispersal limitation and niche differentiation into a single model. Although we could not strictly partition the variance because of the non-linear niche model, we can see that the mixed model has a superior explained variance to the sum of the niche and the neutral models (Table 4.2). For instance, species 2 has 30.1% and 17.0% of the variance explained respectively by the niche and the neutral model. The fraction of the variance explained by the mixed model is 80.3%, 33.2% superior than the sum of the two submodels alone. This

Table 4.2 Performance of different spatial variables to model species distribution with the spatially explicit simulations dataset. A RDA on Hellinger-transformed species abundance is used for the polynomial, the PCNM variables and the predicted seed rain. The predicted seed rain is also used as an explanatory variable in the species specific model (only species > 20 adult individuals in the subplot are modelled – see text for details on the model). PCNM variables are selected with a forward selection procedure with a selection threshold of p = 0.1.

Spatial variables	Variance fraction (%)				
	Total [a]+[b]+[c]	ENV [a]	SPACE [c]	ENV + SPACE [b]	Unexplained [d]
Polynomial	38,6	26,1	12,5	0,1	61,4
PCNM	40,5	24,6	14,4	1,5	59,5
Expected seed rain - RDA	41,6	25,0	15,5	1,1	58,4
		[a]+[b]	[b]+[c]		
Expected seed rain - Average of specific models (±SE)	70,6 ±1,9	37,9 ±3,3	15,7 ±1.8	-	29,4 ±1,9

Figure 4.2 Fraction of variance explained as a function of species abundance in the spatially explicit simulations dataset (modelling with the species-specific non linear models – only species > 20 adult individuals are represented).



situation occurs because when modelling only species abundance as a function of the environment, a species could be absent from a favourable site because of dispersal limitations or overabundant on an unfavourable site because of a mass effect, thus reducing the performance of the niche model. The same logic applies for the neutral model. The combined model is thus superior to the sum of its parts. The performance of the fractions [a]+[b] and [b]+[c] is also underestimated. Consequently, the usage of the predicted seed rain in the species specific models performs a better quantification of dispersal limitations than the use of the polynomial and the PCNM variables.

The usage of species specific models also allows a finer analysis of species distribution, providing finer results on the underlying processes. An example is provided at Figure 4.2, where the fraction of variance explained by the niche model is plotted against the fraction explained by the neutral model. There is a clear trade-off between the two models. Species limited by the environment are not dispersal limited and vice versa. We also plotted the fraction of variance explained by the two models as a function of the abundance (not shown) and found that the most abundant species are only limited by the environment, while the rarest species are mostly dispersal limited. This result would have been impossible to get from typical ordination methods.

4.6 Sapling distribution in northern hardwoods

In our final example, we illustrate with field data how the fraction "space" can be misinterpreted as a quantification of dispersal limitation. The data consists of the abundance of regeneration of *Acer saccharum* Marsh. (ACSA) and *Fagus grandifolia* Ehrh. (FAGR), two common shade tolerant tree species coexisting together in north-eastern America. These species relative abundance is presumably related to light availability and soil properties (Arii and Lechowicz, 2002). FAGR is more shade tolerant (Canham, 1988) and less sensitive to soil base cation availability (Kobe, 1996), but has smaller dispersal capabilities and fecundity than ACSA (Ribbens et al., 1994).

Sampling was conducted in a mature uneven-aged stand located 50 km north of Quebec city, Canada (46°85`, 71°40'W). Spatial coordinates, DBH and species identity were recorded for every tree larger than 4.1 cm at DBH in a plot of 75 X 125m. A more intensive

sampling was conducted in a 30 X 80m subplot. The subplot was divided into a grid of 5 X 5m quadrats. For every quadrat, we recorded the density of seedlings (0-0.3m height) and small saplings (0.3 – 1.0 m height) in a 2m radius subplot and performed a detailed characterization of the environment. Environmental variables include aspects of topography, soil properties, light availability at 1 and 4 meters height and 25 years previous growth of small saplings (a proxy of past light history). The detailed methods are provided in the Appendix.

For simplicity and to provide a comparison with similar studies, we used the RDA in this analysis, assuming a linear relationship between species abundance and the environment. The analysis with only two species does not have the problem of the arch effect explained above. Again, we compare the performance of the polynomial, the PCNM method and the expected seed rain to model species distribution. The expected seed rain is calculated following the method and parameters of Ribbens et al. (1994) for these species. Seed rain is thus predicted by the location of adults in the neighborhood, with their fecundity weighted as a function of DBH. Again, prior to the partitioning of the variance between the environmental and the spatial fractions, the environmental and the PCNM variables were selected with a forward selection procedure at $p = 0.1$.

The fraction of variance explained by the spatial variables differs considerably between the datasets and the different methods (Table 4.3). The polynomial has a constant performance for both seedlings and small saplings. On the opposite, the performance of the PCNM variables differs considerably. The common fraction [b] is much higher relative to the pure spatial fraction for the seedlings in comparison to the small saplings. Finally, the expected seed rain has a low performance for both the seedlings and small saplings.

The comparison of the different methods illustrates two important concerns about the interpretation of the pure spatial fraction [c] and the common fraction [b]. Our perspective on this is not to suggest the above method using the seed rain is the right one (in many cases the dispersal kernel will be impossible to measure), but rather to illustrate how modelling the community spatial structure is not the adequate quantification of dispersal limitations. First, as argued above, the polynomial and PCNM variables are not necessarily descriptors of

Table 4.3 Performance of different spatial variables to model sugar maple and American beech in a northern hardwood forest stand. Species abundances are standardized prior to analysis. All three analyses are performed with a RDA. PCNM and environmental variables are selected with a forward selection procedure with a selection threshold of p = 0.1.

Dataset	Method	Variance fraction (%)				
		Total [a]+[b]+[c]	ENV [a]	SPACE [c]	ENV + SPACE [b]	Unexplained [d]
Seedlings	Polynomial	55,1	7,1	13,4	34,6	44,9
	PCNM	64,0	3,5	5,8	54,7	36,0
	Expected seed rain	44,9	24,1	3,2	17,5	55,1
Saplings	Polynomial	50,8	10,9	13,3	26,6	49,2
	PCNM	62,1	9,6	24,6	28,0	37,9
	Expected seed rain	39,3	16,4	1,8	21,1	60,7

dispersal limitations. The performance of the expected seed rain is much lower than these variables for both the seedlings and the small saplings. Given the elevated fractions [b] and [c] for both the seedlings and saplings, it could have been tempting to conclude that dispersal limitations are more important than environmental differentiation in this dataset. This interpretation has been made elsewhere (e.g. Gilbert and Lechowicz, 2004; Karst et al., 2005; Cottenie, 2005).

The second point is the interpretation of the information contained in the fraction [b] explained conjointly by the environmental variables and the spatial variables. In the situation where the environmental variables are strongly spatially structured, it will be hard to partition the environmental and the spatial fractions with traditional methods. In many cases, such as for the seedlings with the PCNM variables, a large fraction of the explained variance will be in this fraction [b]. In such situations, results are almost meaningless. The usage of the expected seed rain or any other predictor based on neighborhood composition such as competition kernels (Bolker and Pacala, 1997) will facilitate the lowering of the fraction [b], especially in cases where there is a strong spatial structure in the environmental variables.

4.7 Discussion

The canonical ordinations did not efficiently model species differentiation for communities satisfying the limiting similarity predicted from the niche theory (MacArthur and Levins, 1967). The CCA, developed on the assumption of gaussian-shaped niches (ter Braak, 1985), was among the worst methods we tried. The resulting ordinations with the different distance metrics are characterized by a strong arch effect. This issue has been discussed from a long time (see the discussion by Legendre and Legendre, 1998), the important point we want to stress here is how sensitive the model is to the level of niche overlap, and how it could bias the quantification of niche differentiation. Trials with a segmented DCA performed on the deterministic simulations did not either successfully recovered the original structure of the data, neither did non-metric multidimensional scaling (although for a different results; results not shown). The higher performance of ordinations with elevated niche overlap goes against the fact that ecological drift and demographic stochasticity increase with species similarity (Gravel et al., 2006). For these reasons, we

believe these analytical methods are of limited use for this specific question of the relative importance of neutral and niche processes.

Quantifying the spatial structure of a community is also a weak test of neutral dynamics (McGill, 2003). The limitation of this test arises from the fact that 1) there are multiple explanations to the observed pattern and 2) this approach of curve fitting results in biologically non interpretable parameters (McGill, 2003). The analysis of the forest regeneration dataset illustrates well how spatial patterns in vegetation could be wrongly attributed to dispersal limitations. Moreover an implicit condition of this test is the existence of spatial patterns. There is the possibility however that in a neutral community the spatial distribution of some species will not be structured, leading to an incorrect rejection of the neutral hypothesis. For instance, abundant species will not necessarily exhibit a spatially structured distribution, as in communities with low dispersal limitations or low diversified communities. In terms of spatial structure, the adequate prediction of the neutral theory is that the recruitment success at one point in space is strongly correlated to the neighbourhood composition because of dispersal limitations. This prediction must take into account the *a priori* formulation of the dispersal kernel, rather than a posterior fitting of the pattern. We therefore recommend paying careful attention to the interpretation of studies partitioning niche and neutrality under the perspective of the spatial patterns (e.g. Cottenie, 2005).

The species by species analysis is far more efficient to evaluate the relative importance of niche and neutral processes. In our case, we benefited from the exact knowledge of the dispersal kernel and of the shape of the species functional response to the environment. Although we recognize that this is an almost perfect situation that will be hard to find in nature, it did allow us to illustrate the synergistic effect of considering both into a single model. Strong dispersal limitations will result in a species to be absent to some of its favourable sites (Tilman, 1994; Hurtt and Pacala, 1995; Pulliam, 2000). On the other hand, the neighbourhood composition could also contribute to an over-abundance of species on unfavourable sites (the mass-effect perspective, Loreau and Mouquet, 1999). To omit dispersal limitations and the mass effect in a niche model will result in a biased estimation of niche differentiation (for both the fraction of variance explained and the parameters) and vice-versa for dispersal limitations. Moreover, this finer analysis provides new information

that would be otherwise lost in a community-level analysis. It was shown in our simple simulation model that some species will be more limited by the environment, others by dispersal limitations. The more abundant species also tends to be more environmentally restricted than the rarest. This result confirms the hypothesis proposed by Gravel et al. (2006) that once a community is saturated by complementary species, the abundance of the redundant species will be mostly determined by drift. The multivariate framework assumes all species are equal regarding these processes.

Numerous studies have shown how difficult it could be to distinguish patterns predicted by the niche theory from those predicted by the neutral theory (Tilman, 2004; Bell, 2005; Purves and Pacala, 2005; Gravel et al., 2006; Harpole and Tilman, 2006). Mechanistic approaches rather than curve fitting exercises are required (McGill, 2003; McGill et al., 2006). Toward this end, there are new promising statistical techniques such as the ones proposed by Uriarte et al. (2004) and Shipley et al. (2006). It is worthwhile however to insist on the fact that results presented here are not invalidating ordination techniques. They rather stress the importance of knowing the limitations of these methods and to assure their agreement with the tested hypotheses.

4.8 Appendix: Description of the sampling methodology for the forest regeneration dataset

4.8.1 Study site

The study site is located at the Duchesnay forest Station (46°70'-47°00'N, 71°35'-71°45'W), 50 km north of Quebec City. The vegetation of the station is dominated by mature deciduous forest stands with patches of mixed and coniferous stands. The mean annual temperature is 3.4°C and the mean annual precipitation is 1300 mm/yr (Houle et al., 1997). A mature forest stand was selected on representative conditions where the maple-beech community is found. The stand is located on a middle slope, on a tick glacier till deposit good to moderately well drained. The location of the sampling plot was however arbitrarily chosen to have within-plot heterogeneity, based on micro-topography, in order to assure minimal spatial variations in soil properties. The composition of the cover (trees >9.1 cm at DBH) is dominated by sugar maple (55.9% of basal area), American beech (27.0%), *Betula alleghaniensis* Britton (15.7%) and there are traces in the community and its periphery of *Acer rubrum* L., *Acer pensylvanicum* L., *Tsuga canadensis* (L.) Carr., *Abies balsamea* (L.) Mill. and *Picea rubens Sarg.*. The total basal area is 24.9 m²/ha and the largest diameter is 71.1 cm. The most common herbaceous and shrub species were *Lycopodium lucidulum*, *Dryopteris spinulosa, Streptopus roseus*, *Trillium erectum, Oxalis Montana, Clintonia borealis and Taxus canadensis*. Signs of beech bark disease were present, but at the time of the study the disease appeared to have only a minor effect in this forest. The stand could have been subjected to partial harvest prior to the 1950s, as most stands in the region, but there where no evidences of past disturbance on the site and understory saplings of maple and beech between 100 and 200 years old where previously found at this site (Gravel, unpublished data).

4.8.2 Field sampling

The spatial coordinates, DBH and species identity was recorded for every tree larger than 4.1 cm at DBH in a plot of 75 X 125m. A more intensive sampling was conducted in a subplot of 30 X 80m. The subplot was divided in a grid of 5 X 5m quadrats. For every quadrat, we recorded every sapling between 1m height and 4.0cm DBH. New year seedlings

(with cotyledons) density was measured in a 1m² subplot centered on the quadrat. Density of seedlings up to 1m height was measured in a 2 m radius (12.57 m²) subplot centered on the quadrat. Light availability was determined at the center of each quadrat and for heights of 1 and 4m by measuring the photosynthetic photon flux density (PPFD) with a light sensor (LI-190SA point quantum sensor, LICOR, Lincoln, NE, USA) and expressed as the percentage of the PPFD measured simultaneously with a sensor located in a open area less than 250 meters from the study site. Measurements were taken under a cloudy sky following the method of Parent and Messier (1996).One soil sample was taken at the center of the quadrat and combined to three other samples located on opposite directions at one meter from the center of the quadrat. Sampling was done on the first 5 cm of the B horizon. Finally, a disk was sampled at 20 cm height on one sapling per quadrat. Saplings growth history is used as a proxy of past light availability (Chapter 5). The selected sapling was preferentially a beech (easier to read and less ring anomalies), between 2 and 4 cm at DBH and the closest to the center of the quadrat.

4.8.3 Laboratory analysis

Sapling discs were air dried and sanded. Annual growth of the last 25 years was measured at a precision of 0.001 mm under a 40X magnification with an electronic micrometer (Velmex Inc, Bloomfield, N.Y.) coupled with a digital meter (Acurite III, Jamestown, N.Y.). Annual increment was measured along one radius per disc, located at 30° from the longest radius. Visual examination of the discs was done prior to measurements on at least two additional radii where annual rings were clearly readable to identify partial and false rings.

The soil samples were air dried and sieved (2 mm mesh) prior to analysis. Soil pH was measured with a digital pH meter in a solution of 10 g of soil in 20 ml of 0.01 M $CaCl_2$. The exchangeable cations were extracted with an unbuffered solution of 10 g of soil in 100 ml of 0.1 M $BaCl_2$ + 0.1 M NH_4Cl (Amacher et al., 1990). Cations were measured by inductively coupled plasma emission.

CHAPITRE V

CONSEQUENCES OF STOCHASTICITY IN NICHE DIFFERENTIATION FOR COMMUNITY DYNAMICS

Chapitre soumis à la revue Ecology:

Gravel, D., Canham, C.D. and Messier, C. Consequences of stochasticity in niche differentiation for community dynamics.

5.1 Résumé

La théorie sur la coexistence assume généralement une réponse déterministe des espèces à l'environnement, la compétition et la prédation. Il a été argumenté récemment que négliger la variabilité dans ces processus pourrait biaiser les prédictions de modèles de la dynamique des communautés. Utilisant deux variantes d'un simple modèle de loterie qui prédit la coexistence entre deux espèces dans un environnement spatialement hétérogène, nous démontrons que au-delà d'un certain seuil dans la variabilité de l'optimum écologique des espèces, la stochasticité influence fortement la coexistence, le taux de succession, la probabilité d'extinction et la variabilité dans l'abondance des espèces. Par ailleurs, nous démontrons que différentes formes de stochasticité donnent des résultats contrastés, dans certains cas favorisant la dérive aléatoire et l'équivalence écologique, dans d'autres cas contribuant à la coexistence. Les écologistes de terrain testent typiquement des hypothèses sur la différentiation des espèces sur la base de différences statistiques significatives entre les moyennes de traits. Ultimement, des modèles sont nécessaires pour tester comment les composantes déterministes et stochastiques de la différentiation des espèces influencent la dynamique des communautés.

Mots-clés : stochasticité démographique, modèle loterie, dérive aléatoire, storage effect, coexistence

5.2 Abstract

Much of the literature on theories of coexistence assumes that species responses to the environment, competition and predation are deterministic. It has recently been argued that failure to incorporate stochasticity in these processes could bias the predictions of models of community dynamics. Using two variants of a simple lottery model predicting coexistence between two species in a spatially heterogeneous environment, we show that above a threshold level of stochasticity in species optima, stochasticity strongly influences coexistence, rate of succession, probability of extinction and variability in species abundance. Further, we show that different forms of stochasticity can lead to contrasting results, in some cases favouring neutral drift and ecological equivalence, while in others contributing to stable coexistence. Field ecologists typically judge hypotheses related to niche differentiation based on statistical differences between means of traits. Ultimately, models are necessary for tests of how both the deterministic and stochastic components of niche differentiation influence community dynamics.

5.3 Introduction

Niche differentiation reduces interspecific competition relative to intraspecific competition, and thus reduces competitive exclusion (Chesson, 2000; Chase and Leibold, 2003). In models, coexistence occurs when a species is sufficiently differentiated from the dominant species to recover from periods with low abundance (MacArthur and Levins, 1967; Chesson, 2000) and invade new sites (Tilman, 2004). Thus, there is a limiting similarity between species for stable coexistence to occur (MacArthur and Levins, 1967). There are many examples in the ecological literature, dating from the early work of naturalists (e.g. Grinnell, 1917), showing that species do indeed differentiate in their responses to biotic and abiotic conditions. The challenge, of course, is to determine whether the empirically observed differences between species allow for stable coexistence. Traditional statistical methods normally test whether the means of traits that contribute to niche differentiation differ between species. In most cases, however, if sampling is done well enough to reduce "noise" and to increase statistical power, almost all species can be expected to show statistically significant differences in their mean response to any given abiotic or biotic factor. Recently, Clark et al. (2003) have proposed that various sources of uncertainty in species response to the environment could be at least as important in explaining community dynamics as the mean differences among species. They argue that ignoring sources of stochasticity and uncertainty in interspecific trade-offs can lead to conclusions that species differ more than they actually do, and to inaccurate and overconfident predictions in models of community dynamics (Clark et al. 2003).

There is an extensive literature on the dynamics of isolated populations under demographic and environmental stochasticity (e.g. Lewontin and Cohen, 1969; Levins, 1969a; May, 1974; Boyce, 1992; Lande, 1992; Helley and Iwasa, 1998; Kendall and Fox, 2002; 2003; Robert et al., 2003). Those studies generally agree that demographic stochasticity increases extinction risks in small populations, while environmental stochasticity increases extinction risks for both small and large populations. There have been far fewer tests of the consequences of various forms of stochasticity in models of community dynamics. May and MacArthur (1972) and Turelli (1978) examined whether environmental variability could impact species with limiting similarities, and found that weak to moderate

stochasticity can allow an infinite number of species to coexist on an environmental gradient. The storage effect (Chesson and Warner, 1981; Chesson, 1994; 2000b) predicts that random fluctuations in recruitment promote stable coexistence for organisms with overlapping generations. The storage effect applies in temporally, spatially and spatio-temporally fluctuating environments (Chesson, 1985). However, the issue of the effects on community dynamics of individual-level variation (both genotypic and phenotypic) in the large number of traits that can contribute to niche differentiation remains largely unexplored in either theoretical or empirical models.

Our objective in this study is to use a simple model to examine how incorporating stochasticity in niche differentiation alters predictions of community dynamics. Species coexist in the model when their response to the environment is deterministic because they differentiate along an environmental gradient and the environment is spatially heterogeneous. We examine two different forms of stochasticity, as suggested by Clark et al. (2003). The first consists of variability in the response of a single individual to a fixed environmental condition. In a classical statistical approach, a simple example of the response Y of an individual i to the factor X could take the form: $Y_i = \beta X_i + \varepsilon_i$. This model assumes there are true values of Y, β and X. The error term ε is pure noise, usually assuming a normal distribution with mean zero and variance σ^2. In this form of variability, repeated measurements on the same individual in a constant environment will produce different responses over time. We refer to this form of stochasticity as *within-individual* stochasticity. There are many different processes that contribute to the observed error term, including measurement errors and omission of other resources affecting species response. We will focus on the consequences, rather than the multiple causes, of this individual-level stochasticity in response to the environment. Note that this form of variability could be independent among individuals [corresponding to the "stochastic resource" in Clark et al.'s (2003) terminology], or covary among individuals from one time event to another, or from one microsite to another (the "random location effect").

A common but crucial assumption made in many models of community dynamics is that the parameters of a specific response to the environment are common to all individuals of the species, i.e. that there is a true and single value of β. Obviously, this is not the case in

nature where individuals differ because of different genotypes and phenotypes. Therefore, in the second form of stochasticity we will consider, each individual has a unique, deterministic response to *X*, but the population response as a whole is variable; i.e. $Y_i = \beta X_i$ where β is a random variable with a normal distribution $\beta(\mu, \sigma^2)$. As a result, repeated measurements on the same individual would lead to an identical response to a specific environmental factor *X*, but the response would vary between individuals for a constant *X*. We refer to this as *between-individuals* stochasticity, corresponding to the "random individual response" of Clark et al. (2003).

Neglecting either source of stochasticity could have important consequences for population dynamics. The simplest expectation is that for species in a heterogeneous environment, increasing between-individuals stochasticity will reduce effective niche differentiation over the environmental gradient and favour neutral drift (i.e. the weak interpretation of the neutral theory; Bell (2001) and Holt, (2006)). In contrast, based on the framework of the storage effect (Chesson and Warner, 1981), we hypothesize that either a negative or positive covariance in the variability of the functional response to the environment among species at the community scale (i.e. within-individual stochasticity), resulting in recruitment fluctuations over time, will favour coexistence. Moreover, the stability of coexistence will increase with variability in the response to the environment. Finally, we hypothesize that the absence of a covariance structure in the individual stochasticity (due to independence between individuals), will average species performance over the environmental gradient and again favour neutral drift (i.e. a non-directional random walk towards extinction).

5.4 Model description

We simulated a community of two species organized by a lottery competition for space in a spatially heterogeneous environment, using a model presented in our previous work on niche vs. neutral dynamics (Gravel et al. 2006). For convenience, individuals (both adults and juveniles) are discrete and the population is finite. The model is spatially implicit because adults and juveniles are represented on a lattice of 25*25 cells, where every cell has an independent and constant environmental condition E. For computational simplicity, we

assumed dispersal is uniform through space. We examined simulations with spatially explicit dispersal and they revealed no qualitative differences from results using uniform dispersal.

Each cell of the lattice is occupied by a single adult and up to 25 juveniles. When there are fewer than 25 juveniles in a cell (due to juvenile mortality), new juveniles are added in proportion to the adults' relative abundance over the entire lattice. When an adult dies, the new occupant of the cell is the winner from a lottery among juveniles in the cell. We simulated two variants of the model where alternatively only adult or juvenile survival was a function of E (see Table 5.1). The shape of the survival function is Gaussian: $s(E)=\square*\exp[-(E-\square)^2/2\square^2]$, where $\square$ is survival at the niche optimum, $\square$ is the niche optimum and $\square$ is niche breadth. There is no immigration or emigration in the model.

Values of E in each cell of the lattice were determined by random draws from a uniform distribution ranging on an arbitrary scale from 0 to 100. Species A has an optimum ($\square$) at E = 25 and species B at E = 75. Niche breadth ($\square$) was 50 for both species, resulting in limited niche overlap and allowing stable coexistence under the deterministic scenario (see *Results*). Survival at optimum ($\square$) was set at 0.8 for adults and 0.5 for juveniles.

5.4.1 Implementation of stochasticity in niche differentiation

For the between-individual stochasticity, the survival optimum ($\square$) for every individual was drawn from a normal distribution with the mean corresponding to the species' niche and a standard deviation ranging from 0 to 15 (recall that species A has an optimum $\square$ = 25, and species B has an optimum at $\square$ = 75; thus this range of variation corresponds to 0-30% of the mean at $\square$ = 50). The niche optimum was assigned at birth and maintained throughout the lifespan of the individual. We simulated two scenarios; (1) both species A and B have a stochastic functional response, and (2) only species A has a stochastic functional response (see Table 5.1 for a summary of the simulations performed). For simplicity, we kept the mean and the variance constant through time (i.e. no evolution in the populations). It is beyond the scope of this paper to include evolutionary processes such as selection for traits, mutation and inheritance. Clark et al. (2001, 2003) called for full consideration of all forms of uncertainty in empirical models, in order to increase the confidence in their predictions. We note,

however, that this would represent a very significant empirical challenge, since it would require an understanding of the covariance structure for all parameter estimates in the model.

We implemented within-individual stochasticity by randomly varying the environment in each cell over time. An exact implementation of this form of stochasticity would have required the addition of a random deviate to every individual survival probability. The species response to the environment is, however, bounded between 0 and κ, which would require a very complicated specification of the probability distribution of the deviates. Random fluctuations in the environment (E) produce qualitatively similar results. We simulated three variants of the within-individual stochasticity: (1) positive covariance among species, (2) negative covariance and (3) no covariance. Under positive covariance, random fluctuations in the environment have similar benefits on average survival of both species across the plot (e.g. similar response to year-to-year fluctuations in precipitation for two plant species differentiated by pH tolerance). Alternatively, in the case of negative covariance, year-to-year fluctuations in the environment favour one species and disfavour the other. Within-individual stochasticity with covariance among species was simulated by adding a single deviate D, picked from a normal distribution at each time step, to the background level of E for each cell. Positive covariance between species is generated by opposing the sign of the random deviate D between species. This makes average performance of both species either closer or farther from their optima, thus creating positive covariance. In the alternate case, the sign of the random deviate D is the same for the two species. The fluctuation in survival is then on average favourable for one species while unfavourable for the other species because the environment in the grid cell is now either closer to the optimum for species A or species B. For the scenario with no covariance, a random deviate D was drawn independently for every individual (no covariance between species and individuals). For the three scenarios of within-individual stochasticity, the niche optimum was deterministic (i. e. all individuals of a given species have the same niche optimum).

5.4.2 Data analysis

The analyses focus on five aspects of community dynamics: coexistence, extinction probability, successional rate, relative abundance at equilibrium and variability in relative

abundance. Simulations were initiated with species A at 10% relative abundance and species B at 90%. Given that half of the cells are favourable for species A, it must be able to increase in relative abundance when at low initial abundance for stable coexistence to occur (Chesson, 2000). Simulations were run for 10 000 time steps - many times longer than necessary to reach equilibrium relative abundance and a sufficient time to reach extinction by a random walk under the extreme case of a neutral model (Hubbell, 2001). We replicated each scenario 50 times and then fitted a model for the relative abundance of species A over time:

Eq. 1 $$R(t) = \theta\alpha^t + \omega + \varepsilon$$

The sign of □ determines whether there is stable coexistence or not (positive or negative growth). Successional rate is determined by the magnitudes of □ and □. The parameter ω is the relative abundance of species A at equilibrium and □ is the variability in relative abundance over the time series. We also recorded how many times out of the 50 replicates there was extinction of either one of the species.

5.5 Results

Incorporating even very high stochasticity in species response to the environment does not prevent coexistence based on Chesson's (2000) invasibility criterion of positive population growth when at low abundance (Figure 5.1A-B). The one exception is when only one species shows variability among individuals in its response to the environment. In this situation, the species with the stochastic response will tend towards extinction. These results occurred in models with differentiation in mortality among either adults or juveniles.

While positive population growth rates when at low abundance are a sufficient criterion for coexistence in a deterministic model, our results indicate that this is not necessarily sufficient when stochasticity is considered, given the greater extinction risks with increasing stochasticity (Figure 5.1C-D). Although the average population growth rate at low abundance is positive in most scenarios, suggesting that species differentiation leads to stable coexistence, increasing levels of stochasticity after reaching a certain threshold produced numerous runs in which one of the species became extinct. Species A tends to get more often excluded than species B because it starts at low abundance (not shown), but species B is

Table 5.1 Summary of the simulation scenarios performed. Each scenario is performed for the model with differentiation at the adult stage and at the juvenile stage.

Scenario	Source of stochasticity	Structure
1	Between-individuals	Species A and B
2	Between-individuals	Species A only
3	Within-individuals	Positive covariance among species
4	Within-individuals	Negative covariance among species
5	Within-individuals	No covariance

Figure 5.1 Properties of community dynamics with increasing stochasticity (standard deviation) in species' responses to the environment. The upper panels (A and C) are results from simulations with stochasticity in adult differentiation; the bottom panels (B and D) are based on juvenile differentiation. On the left: criteria for stable coexistence based on the direction of population growth over time (theta, see Eqn. 1). Coexistence occurs for theta > 0. On the right: extinction rate, based on the proportion of simulations with extinction of either Species A or B out of 50 replicates per scenario. The five lines are for the five forms of stochasticity listed in Table 5.1: solid circles = between-individual stochasticity for both Species A and B; open circles = between-individual stochasticity for only Species A; solid triangle: within-individual stochasticity with positive covariance between species; open triangle = within-individual stochasticity with negative covariance between species; closed squares: within-individual stochasticity with no covariance between species. Default parameters: adult maximum population size = 625 individuals; run length = 10 000 timesteps; E ranges uniformly from 0 to 100; distance between modes = 50; niche breadth = 50; initial relative abundance of species A = 10%; survival rate at optimum = 0.8 for adults and 0.5 for juveniles.

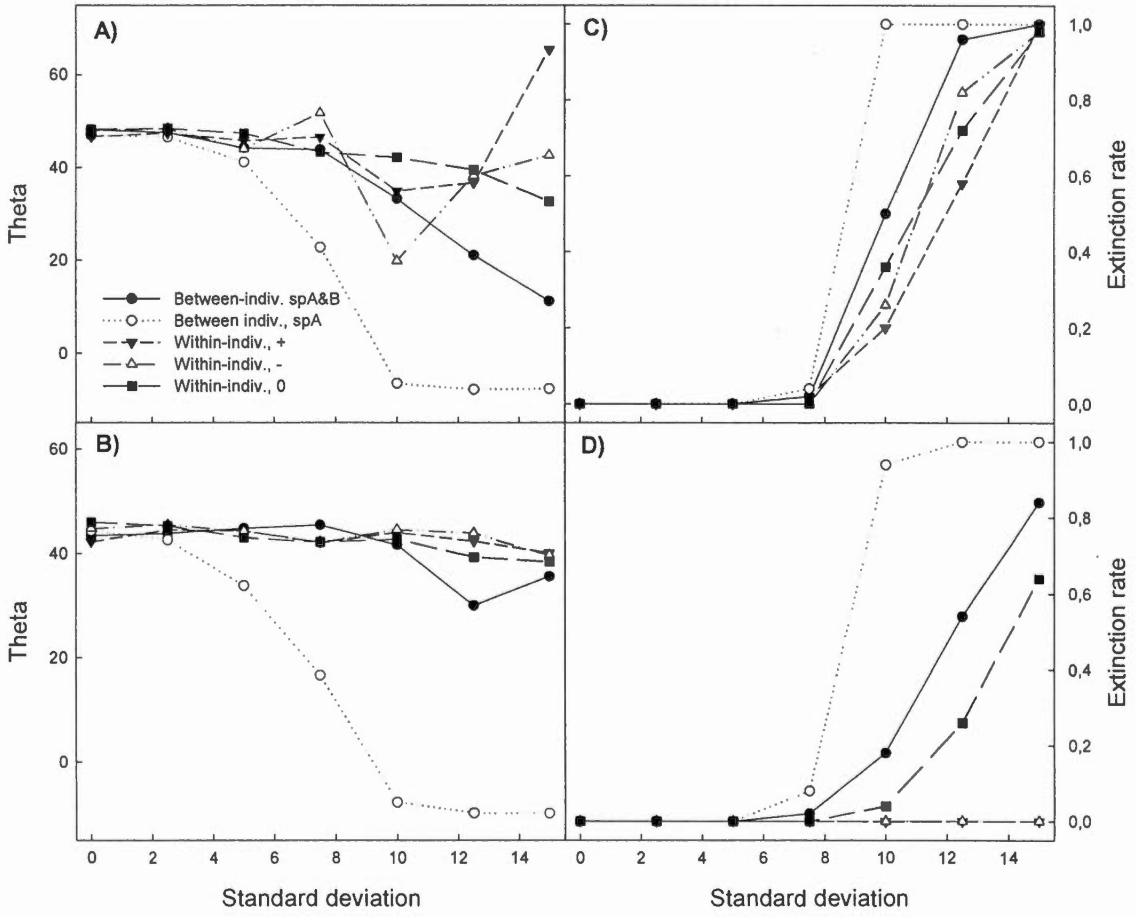


Figure 5.2 Properties of community dynamics with increasing stochasticity in species' responses to the environment (suite). The five lines are for the five forms of stochasticity listed in Table 5.1. Line types as in Fig. 5.1. The upper panels (A and C) are based on differentiation in adult survival; the bottom panels (B and D) are based on juvenile differentiation. On the left: rate of succession expressed by the amount of change in relative abundance (%) after 100 time steps. On the right: residual variability (□) after fitting the model of relative abundance over time (see Eqn. 1). Default parameters are as in Fig. 5.1.

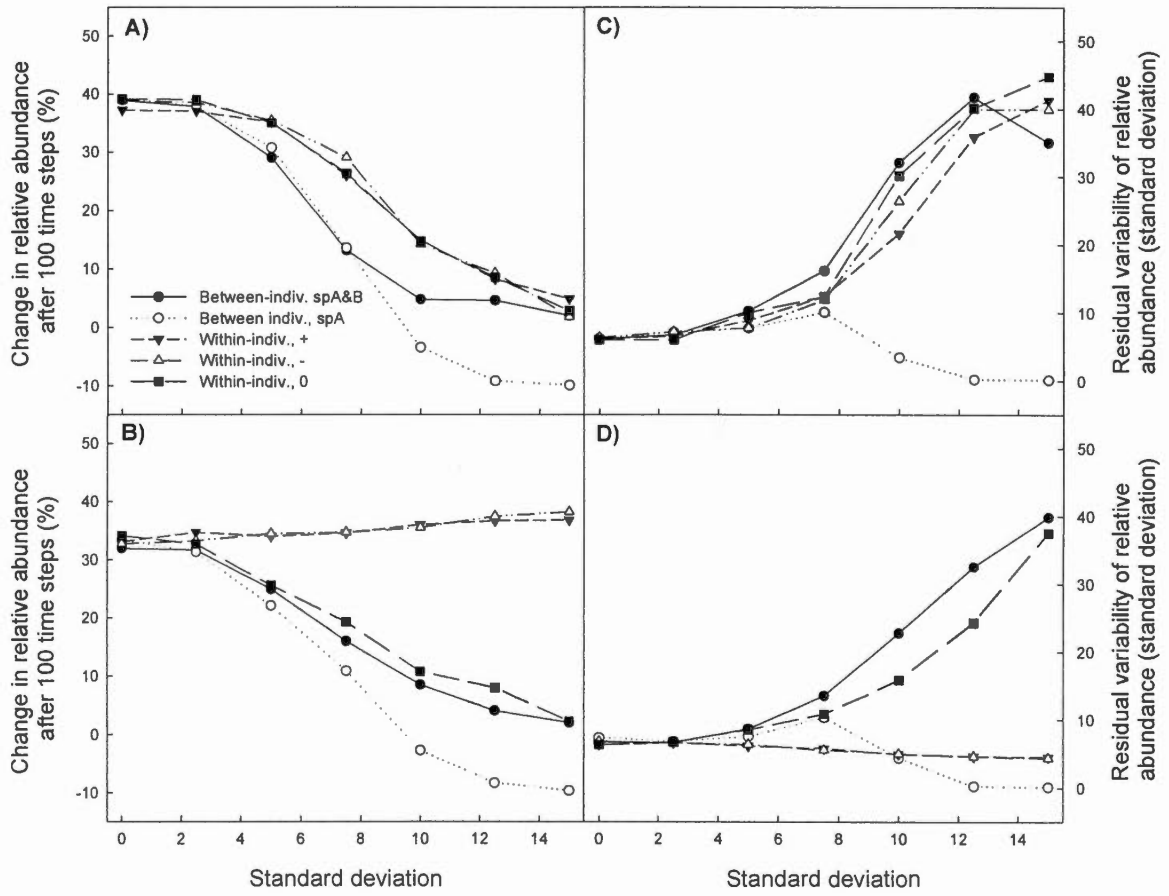
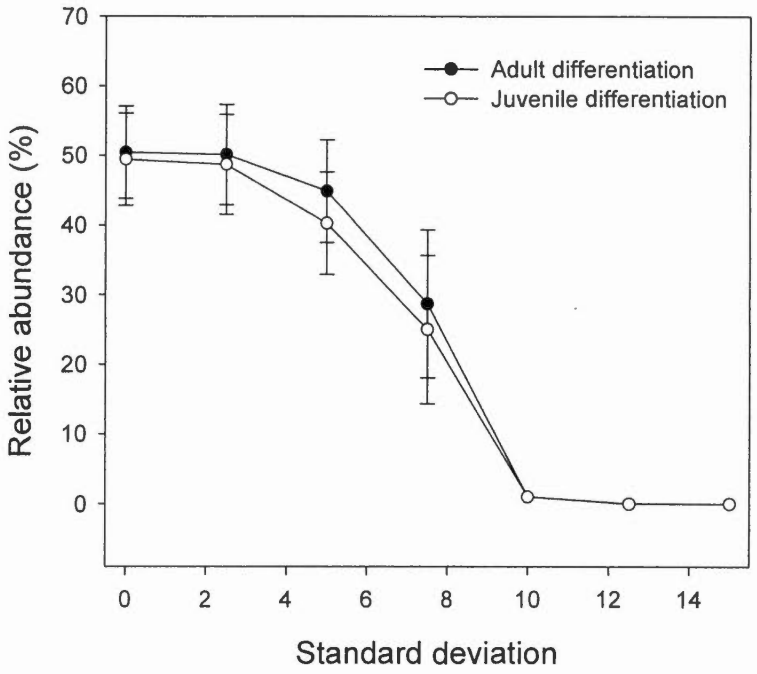


Figure 5.3 Relative abundance of species A after 10 000 timesteps for the scenario with only species A having stochastic response to the environment, with increasing stochasticity in species' responses to the environment. Default parameters are as in Fig. 5.1. Solid circles are based on differentiation in adult survival; open circles based on differentiation in juvenile survival.



excluded, on average, in 25-30% of the runs. Thus, even if there is a stabilizing force that drives, on average, species of low abundance to increase in density, this may not be sufficient to prevent random extinction when stochasticity is considered. All sources of stochasticity, when at high levels, drove species toward extinction when the differentiation occurred among adults (Figure 5.1C). However, when the juveniles were differentiated, only between-individuals stochasticity and independent within-individuals stochasticity resulted in random exclusion (Figure 5.1 D). There were no exclusions when there was covariance among species (either positive or negative) for the model with juvenile differentiation. When only one species has a between-individual stochastic response, there were an increasing number of extinctions with increasing stochasticity. However, only the species with the stochasticity in survival was excluded.

The rate of succession was reduced by increasing stochasticity in species response to the environment (Figure 5.2A-B). All forms of stochasticity for the model with adult differentiation slowed the rate of succession, until it converges asymptotically to zero. For the scenario with only one species having between-individual stochasticity, rate of succession was progressively slowed, and eventually reached negative values (species A goes extinct), consistent with the above results. Results were similar for the model with juvenile differentiation and between-individuals stochasticity and independent within-individual stochasticity. In contrast, for the model with juvenile differentiation, the rate of succession increased slightly in response to within-individual stochasticity with either positive or negative covariance between species.

The variability in species relative abundance increased in response to most forms of stochasticity (Fig. 5.2C-D), except when only one species showed variability between-individuals in its response to the environment, and for the model with differentiated juveniles when within-individuals stochasticity co-varied between species. Our expectation that stochasticity leads to a deterministic exclusion of the species with variable niche optimums is confirmed by a decreasing variability in relative abundance in response to increasing stochasticity.

Finally, the simulations confirm the disadvantages of a variable niche optimum in a two species competition when the opposite competitor has a deterministic response (Fig. 5.3). In all simulations, the model resulted in stable coexistence of species in the absence of stochasticity in the response to the environment (standard deviation = 0 in Fig. 5.1-3). This is because in our model species A and B have an equal amount of favourable environment, and share an equal part of the available sites. However, increasing between-individuals stochasticity for only one species causes a progressive decline in the relative abundance of that species, and increases variability in its abundance, until it inevitably tends toward extinction.

5.6 Discussion

In all of the simulations, above a threshold level of stochasticity in species optima, stochasticity strongly influenced coexistence, rate of succession, probability of extinction and variability in species abundance. Further, the simulations show that different forms of stochasticity can lead to contrasting results, in some cases favouring neutral drift and ecological equivalence, while in others contributing to stable coexistence. Stochasticity in species' response to the environment thus resulted in community dynamics remarkably different from simulations with a deterministic response. Our models thus provide support for the contention of Clark et al. (2003) that failure to consider the implications of stochasticity in niche differentiation can bias predictions of species coexistence and community dynamics by deterministic models.

Our results can be interpreted in terms of both Jensen's inequality (Ruel and Ayres, 1999) and synchronized fluctuations in recruitment at the population level. Jensen's inequality has numerous applications in ecology, and is commonly used to understand extinction risks under increasing demographic and environmental stochasticity (Ruel and Ayres, 2000; Kendall and Fox, 2002; Boyce et al., 2006). The inequality states that for every non linear function f(x), when x is a random variable with mean $\bar{x}$, then the resulting $\overline{f(x)}$ will be unequal to $f(\bar{x})$.

Consider a situation in which stochasticity in the response to the environment does not result in synchronous fluctuations in recruitment at the population level. The deviation in the survival probability of an individual at a site is independent from every other individual in the population for a single time step (i.e. our scenarios with independent within-individual stochasticity and scenarios with between-individuals stochasticity). In our model, the abundance of a species among juveniles, or alternatively the presence of an adult, depends on a Gaussian shaped survival function. As a result of Jensen's inequality, the average survival probability of a species will be lower than the survival probability of the average E. The effect on the outcome of interspecific competition will depend on how this affects the probability of survival of the two species relative to each other. In the models with differentiation in adult survival, this will affect the capacity of a species to successfully occupy favourable sites. In the models with differentiation in juvenile survival, it will affect the ability of a species to compete for vacant sites.

What happens when both species have a between-individuals stochastic functional response to the environment? Again, as a result of Jensen's inequality, increasing stochasticity will reduce fitness inequalities between the two species and promote drift. In effect, this form of stochasticity reduces both inequalities in population growth rates across space, and the strength of niche differentiation as coexistence mechanisms. Even if the species are never truly ecologically equivalent in the range of stochasticity we simulated, under elevated stochasticity population growth rates at low abundance are too low to reliably recover from declines in abundance caused by random events. The net result is a random walk towards extinction. Our interpretation is consistent with the observation of a declining successional rate with increasing stochasticity in the simulations. It is also consistent with the findings of May and MacArthur (1972) on the capacity of invaders to colonize empty niches with increasing environmental stochasticity.

In the case where only one species has a stochastic response to the environment (between-individuals), the species with the variable response has a lower competitive ability. This situation also arises as a result of Jensen's inequality. At environmental conditions corresponding to the niche optimum of the species with the deterministic response, variations in the optimum of the focal species could either increase or decrease this species'

competitivity, but it would never be superior to the species with the deterministic response. On the other hand, at the optimum of the species with the stochastic response, variations in the optimum could only decrease its recruitment probability relative to the other species. Thus, on average, increasing the variability among individuals of only one species will decrease the recruitment probability for that species. If the variability in the response is not too strong, the resulting small decline in competitive ability will only affect relative abundance and the successional rate. With greater stochasticity, eventually there will be rapid competitive exclusion because of strong competitive inequality on all sites.

The consequences of stochasticity in niche differentiation differ when it creates fluctuations in recruitment because of a covariance among species. The overlapping of generations results in a nonlinear relation between population growth and competition (Chesson and Warner, 1981; Chesson and Huntly, 1989). In communities at the carrying capacity, such as here where replacement obeys a zero-sum rule, the growth of a species will always be limited by the amount of resource left vacant by the death of other species. Consequently, a rare species has a potential per capita growth rate superior to that of an abundant species. This will make the per capita growth rate during favourable environments higher for the rare than for the abundant species (Chesson and Warner, 1981; Chesson and Huntly, 1989). Because of Jensen's inequality, two species could have a positive growth rate when at low abundance if recruitment varies randomly, even if one species is superior on average. This mechanism of coexistence is commonly referred to as the "storage effect" (Chesson and Warner, 1981). This result is in clear contrast with population studies that propose that environmental stochasticity increases extinction risks (e.g. Lewontin and Cohen, 1969; Levins, 1969a; Lande, 1993; Helley and Iwasa, 1998; Robert et al., 2003; but see Higgins et al., 2000).

The results of simulations with structured within-individual stochasticity presented here are in close agreement with the analysis of the lottery models with overlapping generations by Chesson and Warner (1981). Recruitment fluctuations have a stabilizing effect on coexistence, but this not true for fluctuations in adult death rate (Chesson and Warner 1981). In our simulations, since the model structure allowed coexistence in the absence of stochasticity in the functional response, increasing fluctuations in recruitment

added another mechanism of coexistence. Since there was already coexistence in the absence of recruitment fluctuations, only a weak increase in community stability was observed with increasing stochasticity in differentiation among juveniles. The emergence of a storage effect from structured within-individuals stochasticity, however, must also be considered in the situation where there is no niche differentiation along an environmental axis. The absence of any differentiation would not promote coexistence, but careful attention should be accorded to the "noise" in the species response to the environment. In the situation where the residuals were structured over time or space, then it could lead to stable coexistence.

Chesson and Warner (1981) also demonstrated that if adult death rates are negatively correlated between species and tend to take extreme values, then one species will be excluded by chance. We also observed this behaviour in simulations with negatively covarying within-individual stochasticity in the model with differentiation among adults. In this situation, increasing stochasticity has effects similar to the findings of studies looking at the consequences of environmental stochasticity on population extinction risks (Lande, 1993; Helley and Iwasa, 1998). The risk of extinction from variability in adult survival will depend on the relative magnitude of growth rate at low abundance, and the frequency of extreme random reductions in population size (Lande, 1993). In the situation where both species are characterized by elevated stochasticity in survival, demographic variations offset the stabilizing effect of niche differentiation and result in unpredictable species dynamics.

This study has important consequences for the interpretation of niche differentiation documented in field studies. Clark et al. (2003) and Clark (2005) stressed the importance of a better understanding of the error structure in the analysis of empirical data. They emphasize that error terms typically contain not only measurement error, but also include biological components that could have important implications for community dynamics, and suggest that field ecologists need to devote greater effort (through the use of hierarchical models) to distinguishing between different sources of error. A statistically significant difference between species does not always reflect biologically meaningful differentiation. For instance, if the functional response used in this study had represented plant species survival as a function of soil pH for two species, at the maximum level of between-individuals stochasticity simulated one would have found a highly statistically significant ($P<0.001$)

difference between species with a traditional t-test comparing species optimums. However, if stochasticity is taken into account, the differences in niche optima were far from sufficient to allow a stable coexistence between species. A statistical test, no matter how rigorous the analysis, is just a tool in the process of testing scientific hypotheses. In the above example, the statistical test (H0: optimum of A = optimum of B) does not allow an adequate testing of the scientific hypothesis (H0: difference in optimum of A and B is not the mechanism of their coexistence in a heterogeneous environment). We agree with Hubbell (2001) that finding functional differences between species in pot experiments do not necessarily support the conclusion that the species coexist through niche differentiation. Indeed, the results presented here challenge the traditional search for niche differentiation in field studies, and suggest that models that include stochasticity must play an important role in assessing the significance of field results.

The different forms of stochasticity considered in our model off-set deterministic niche differentiation, and in many cases result in what would appear to be neutral dynamics. This is yet another explanation for the ability of neutral models to predict patterns of species relative abundance (Hubbell 2001; Volkov et al. 2003), even when the underlying community exhibits niche structure (Gravel et al. 2006). Hubbell (2005, 2006) argued that the elevated stochasticity in neighbourhood composition of tropical forest trees resulting from dispersal limitations could favour the evolutionary convergence of ecologically equivalent species. He illustrated his hypothesis with the extremely high variability in growth history found in a pioneer tropical tree species. Given the high degree of overlap of species along the survival-growth trade-off in tropical forests (Condit et al., 2006) and the high variability in their demographic parameters, it is not surprising to observe that these forests can be characterized by neutral models.

CHAPITRE VI

SHADE TOLERANCE, CANOPY GAPS AND MECHANISMS OF COEXISTENCE AMONG FOREST TREES

Dominique Gravel, Charles D. Canham, Marilou Beaudet et Christian Messier

6.1 Résumé

Parmi les caractéristiques les plus générales de la dynamique des forêts à travers le monde se trouvent l'hétérogénéité de l'environnement lumineux résultant de la formation de petites trouées dans la voûte forestière et la différentiation des espèces dans leur réponse à la disponibilité de la lumière. L'idée que les petites trouées contribuent au maintien de la diversité des espèces en forêt est un paradigme établi en écologie. Sa généralisation aux forêts du monde le rend extrêmement puissant et attirant. Néanmoins, il n'y a pas à ce moment une compréhension éclairée des mécanismes impliqués dans la coexistence basée sur la formation de trouées et la différentiation des espèces en termes de tolérance à l'ombre. Notre objectif dans cette étude est d'identifier de façon plus claire quels sont les mécanismes qui permettraient la coexistence grâce au compromis entre la survie en sous-couvert et la croissance à lumière élevée (un trait distinguant les espèces de différentes tolérances à l'ombre) et à l'hétérogénéité spatiale et temporelle de la lumière créée par les trouées. Nous développons un cadre théorique de la dynamique forestière résultant de petites perturbations, et ce à partir des principes généraux de la théorie de la coexistence dans des environnements variables. Nous vérifions par la suite les prédictions de cette théorie à l'aide d'un simple modèle de simulation de la dynamique forestière. Les résultats obtenus démontrent que l'hétérogénéité temporelle et spatiale créée par les trouées permet la coexistence en vertu des mécanismes nommés « relative non-linearity » et « storage effect ». Toutefois, les fluctuations temporelles de la lumière à elles-seules ne permettent pas la coexistence de plus de deux espèces, au contraire de ce qui est communément assumé dans la littérature. Les variations spatiales dans la synchronisation et l'intensité des perturbations permettent la coexistence de trois espèces dans un espace très réduit de paramètres. Le taux d'extinction est néanmoins extrêmement lent et il y a une coexistence transitoire d'un large nombre d'espèces pour une période de temps très étendue.

Mots-clés : dynamique des forêts, tolérance à l'ombre, coexistence, trouées, non-linéarité relative, storage effect

6.2 Abstract

Among the most general features of forest dynamics worldwide are the occurrence of canopy gaps, and the differentiation of forest tree species in their response to heterogeneity in light and other resources within gaps. The belief that canopy gaps are important for the maintenance of tree species diversity is a longstanding paradigm in forest ecology. Its generalization to temperate, tropical, and boreal forests worldwide makes it extremely powerful and appealing. The assumption that canopy gaps create a range of conditions for regeneration, and thus allow niche differentiation, is intuitively appealing, but there have been no formal theoretical tests of whether and under what conditions this process allows coexistence. Much of the empirical research on niche differentiation in response to gaps has focused on evidence for an interspecific tradeoff between low light survival and high light growth. Our objective here is elucidate the mechanisms of coexistence of forest trees species based on the low light survival/high light growth trade-off (a trait that differs among species of different shade tolerances) as a consequence of spatial and temporal heterogeneity in light availability created by canopy gaps. We develop a theoretical framework of forest dynamics driven by small-scale disturbances from principles of a general theory of species coexistence in variable environments. We then test the predictions with a simple simulation model of forest dynamics. Temporal and spatial heterogeneity in light conditions that result from canopy gaps allow stable coexistence because of two different mechanisms: "relative non-linearity" and the "storage effect". Temporal fluctuations in light availability alone, however, can allow the stable coexistence of only two species, and thus can not constitute an important general mechanism for coexistence of forest trees. Spatial variation in disturbance synchronicity and intensity allows three species to coexist in an extremely narrow parameter space. The rate of extinction is, however, extremely slow and there is transient coexistence of a larger number of species for a long period of time. The tradeoff between low light survival and high light growth is only one of the many possible strategies by which trees may differentiate and coexist along a disturbance gradient. We suggest that mechanisms favouring unstable coexistence should be considered as well.

6.3 Introduction

In many forest ecosystems, light availability is the major constraint on tree growth and survival, and an important axis for differentiation of the ecophysiology, architecture, and demography of tree species (Pacala et al., 1996). There have been extensive efforts to document canopy disturbance regimes and the resulting heterogeneity of light availability in forests worldwide (e.g. Runkle 1981, 1982; Brokaw, 1982; Denslow, 1987; Canham et al., 1990; Yamamoto, 1989; and Kneeshaw and Bergeron, 1998). Many studies have documented a trade-off in the demography of juvenile trees along a light gradient. At one extreme are species with juveniles that have elevated survival rates under low light conditions but only moderate response to canopy openings. At the other extreme are species with juveniles that experience high mortality under low light but have a strong growth response to canopy openings (Canham, 1989). This tradeoff between low light survival and high light growth has been reported in tropical, temperate and boreal forests (e.g. Hubbell and Foster, 1992; Pacala et al., 1996; Kobe and Coates, 1997; Wright et al., 1998; Kobe, 1999; Baraloto et al. 2005; Gilbert et al., 2006; Kneeshaw et al., 2006) .

The idea that canopy gaps contribute to the maintenance of tree species diversity is a longstanding paradigm in forest ecology (Ricklefs, 1977; Denslow, 1980; 1987; Poulson and Platt, 1989; Runkle, 1989; Hiura, 1995; Pacala et al., 1996; Hubbell et al., 1999; Brokaw and Busing, 2000). Its generalization to forests around the world makes it extremely powerful and appealing. It is unclear, however, by which mechanism canopy gaps maintain diversity. The "gap theory" of forest dynamics (Yamamoto, 1992) is a mix of different, largely intuitive, hypotheses on the maintenance of species diversity. In one sense, canopy gaps are thought of as small-scale disturbances that reset community dynamics before competitive exclusion is achieved by the most shade tolerant species (the R* rule, Tilman 1982). More generally, coexistence could be maintained by a wide range of gap-phase related processes, including the generation of a mosaic of small-scale patches at different phases in succession (Jones, 1946; Watt, 1947; Levin and Paine 1974, Forcier, 1975; Connell, 1978), demographic niches (Pacala and Rees, 1998; Rees et al., 2001; Condit et al., 2006), species sorting along a gradient of gap size (Kohyama, 1993; Hubbell et al., 1999), within gap partitioning (Ricklefs,

1977; Denslow, 1980, 1987), the regeneration niche (Grubb, 1977) or different strategies to access the canopy (Canham, 1990; Poulson and Platt, 1996).

Despite the enormous amount of empirical research on gap-phase dynamics in forests worldwide, there are no formal theoretical studies that rigorously identify the mechanisms and conditions under which small-scale disturbances promote species coexistence. The lack of a formal theory of forest dynamics based on canopy gaps and shade tolerance differentiation may explain conflicting results of studies testing the role of canopy gaps in maintaining species diversity (see Hiura, 1995; Hubbell et al., 1999; Brokaw and Busing, 2000; Molino and Sabatier, 2001; Schnitzer and Carlson, 2001; Condit et al., 2006). Thus, a clear understanding of the mechanisms involved in coexistence of tree species based on canopy gaps and shade tolerance is essential to formulate testable predictions in the field.

Our objective in this study is to identify the formal mathematical mechanisms of coexistence of forest trees based on the low light survival/high light growth trade-off and heterogeneity in light availability created by canopy gaps. The first mechanism we consider is known as "relative non-linearity" (Chesson, 1994), and it relies on temporal heterogeneity. Under this mechanism, coexistence is achieved through a trade-off in competitive abilities under variable and constant competitive conditions. It is one of the mechanisms behind the intermediate disturbance hypothesis (Roxburgh et al., 2004). The second mechanism is the "storage effect" (Chesson and Warner, 1981), and is based on spatial heterogeneity generated by asynchronicity in disturbance events and variability in their intensity, respectively. This mechanism is typically associated with the shifting successional mosaic hypothesis (Jones, 1946; Watt, 1947; Forcier, 1975; Connell, 1978; Bormann and Likens, 1979) and the species sorting hypothesis (Kohyama, 1993; Hubbell et al., 1999). The spatial storage effect has also been explored in the context of spatial variation in shade tolerance related to soil heterogeneity (John et al., 2007). For either of the two mechanisms, when there is a spatial component we will also consider the impact of dispersal limitation on species coexistence.

Here, we develop a theoretical framework for forest dynamics in a variable environment based on the general theory of coexistence in variable environments proposed by Chesson (1994, 2000a,b). We then use a simple simulation model of forest dynamics to

develop predictions on the relationships between different sources of heterogeneity and the shape of the growth/survival tradeoff allowing species coexistence.

6.4 Theory of forest dynamics in a variable environment

The following theoretical framework is an application to forest dynamics of the general theory of species coexistence in variable environments synthesized by Chesson 2000a (based on Chesson 1994 and 2000b). Here, we simply interpret the parameters of this general theory for the special case of forest dynamics. Chesson (2000a) distinguishes two broad classes of coexistence mechanisms: 1) fluctuation-independent and 2) fluctuation-dependent mechanisms. Fluctuations in the environment (factors affecting a species response to competition, such as fecundity or juvenile survival) and in competition could be temporal, spatial or both. There are two distinctly different fluctuation-dependent mechanisms of coexistence: relative non-linearity and storage effect. These mechanisms are represented in the following model:

Eq. 1.

$$\overline{r_i} \approx \overline{r_i}' - \Delta N + \Delta I$$

The term $\overline{r_i}$ is the average long term per capita growth rate of species i when at low abundance (i.e. an invading species). The first term on the right-hand side of Eqn. 1, $\overline{r_i}'$, is the combined effects of fluctuation-independent mechanisms and fitness differences among species in the absence of fluctuations. The terms ΔN and ΔI are the effect of relative non-linearity and of the storage effect, respectively (defined below). For stable coexistence to occur among two species, both species must have a positive growth rate when at low abundance. In a two species community of forest trees, without fluctuation-independent mechanisms, the mean fitness difference is positive for the most shade tolerant species and negative for the most shade intolerant, given that the most shade tolerant species will sustain its population at lower light availability. An example of a fluctuation-independent mechanism would be niche differentiation in requirements for seedling establishment along a relatively fixed gradient of soil texture. Aspects of regeneration niches (Grubb, 1977) that

depend on effects of canopy gaps, however, represent a fluctuation-dependent process because light and soil resource conditions will vary over time. In general, for gap-phase processes to contribute to coexistence, they are expected to act via one of the two fluctuation-dependent mechanisms.

It is commonly assumed that the per capita growth rate of a population is a non-linear function of a limiting factor related to competition intensity. Following the early work of Armstrong and McGehee (1980), Chesson (1994) showed that stable coexistence could result from variation in this limiting factor when at least one species has a non-linear response to it. Chesson (2000a) defined the effect of relative non-linearity with the following approximation of the long-term low-density per capita growth rate of a species *i:*

Eq. 2. $$\Delta N \cong b_i(\tau_i - \tau_s)V_i(F)$$

where the parameter b is the rate at which the per capita growth rate declines as resources decline (proportional to R*), τ measures the departure from linearity of the growth response to the limiting factor F, and $V_i(F)$ is the variance in the limiting factor F experienced by the species i when at low abundance and species s is the resident. Depending on the signs of the respective τ (concave or convex functions of F), ΔN could either favour coexistence or competitive exclusion. This effect arises from Jensen's inequality: because of the relative non-linearity of the per capita growth function, variance in the limiting factor causes one species growth rate to increase relative to the other species. An important aspect of this model is that the magnitude of the effect of relative non-linearity scales with the variance in F.

In terms of forest dynamics, the limiting factor the most affected by canopy disturbances is light availability, although canopy gaps also alter soil resource availability (e.g. Mladenof 1988). By definition, the most shade tolerant species will have higher per capita population growth rate at low light availability than the shade intolerant species, largely because of greater low light survival by the shade tolerant species. At higher light availability, however, the per capita growth rate will be greater for the intolerant species

because of higher individual plant diameter and height growth rates. Since both survival and growth of individuals are usually non-linear functions of light availability (Pacala et al., 1996), the per capita growth rate as a function of light availability is also expected to be a non-linear function, with the most intolerant species having the higher □. Consequently, although the R* rule predicts the shade tolerant species to be the competitive dominant, the variance in light availability increases the growth rate of the intolerant species more than the tolerant one. Chesson (1994) demonstrated that this relative non-linearity effect has the potential to maintain the stable coexistence of two species despite one being, on average, a superior competitor. This theory predicts that the fitness difference (R* or here survival at low light availability) between coexisting species will increase with variability in light availability. It also predicts that the fitness difference will also increase with relative non-linearity, which is affected by species dissimilarity along the low light survival/high light growth trade-off axis. One unfortunate consequence of this mechanism, however, is that it also predicts that only two species could coexist through temporal variability in light availability (see Chesson 1994 for details). Competitive exclusion will lead to the selection of the most dissimilar species in their □ because it maximises the strength of coexistence.

The second mechanism of coexistence in variable environments, and perhaps the one with the most variants in forest dynamics, is the storage effect. The storage effect is a mechanism of coexistence that allows a species that is, on average, competitively inferior to coexist with a superior competitor by the storage of the benefits that accrue during periods of high recruitment. This process prevents dramatic population losses during periods of low recruitment. The same reasoning applies to spatial variation in recruitment. The storage effect applies when species response to competition (e.g. competition for light among forest trees) is affected by an environmental factor that varies spatially (e.g. soil fertility). The storage effect in Eq 1. was defined as follows by Chesson (2000a):

Eq. 3.

$$\Delta I = \frac{b_i(1-\rho)(-\gamma)\sigma^2}{n-1}$$

The parameter □ measures the correlation between species responses to fluctuations in the environment, □ measures the buffer against population growth (e.g. longevity of adult trees – negative for strong buffering) and □² is the variance in the environment. Note that the "environment" refers to a factor affecting a species response to competition. An important caveat here is that species must be differentiated in their response to the environment for the storage effect to apply. The more dissimilar the species are in their response to the environment, the stronger the storage effect will be. As in the case of relative non-linearity, the effect of the storage mechanism on the long term population growth rate again scales with the amount of variability in the environment.

It is important to note that the storage effect does not apply in the case where there is only temporal variation in light availability created by canopy gaps. In this case, only the intensity of competition varies through time, while the environment is constant. There are, however, several other ways in which the storage effect could apply in forests. The parameter □ decreases with any source of spatial variability in recruitment, either because of environmental variability or dispersal limitations. One example would the species response to spatial heterogeneity in soil fertility (Kobe, 1996; Russo et al., 2005; John et al.., 2007). For instance, if the survival function of only one species is sensitive to soil pH, then □ will tend to zero (hereafter called the "soil-related" storage effect). Another source of spatial variability in the species per capita growth rate is due to asynchronous phases of succession following canopy disturbances (i.e., the shifting successional mosaic hypothesis). Variation in disturbance intensity can also result in variation in recruitment favourability for different species across space (the species sorting hypothesis). In all of these cases where there is spatial variability in population growth rates, we must consider dispersal limitations that will buffer the gains a species could make in a favourable environment (□) and thus favour the storage effect. The storage effect thus predicts larger differences in low light survival among coexisting species with 1) increasing soil heterogeneity, 2) asynchronicity in disturbance among sub-populations, as well as with 3) increasing spatial variability in disturbance intensity and for all of these with 4) the amount of dispersal limitation.

6.5 Model description

We use a discrete simulation model to allow us to incorporate essential aspects of forest dynamics. Forests are obviously far more complex than the general community model used to develop the theory of coexistence in variable environments (Chesson, 1994; 2000b). We are interested to see if the predictions from this theory will hold in a more complex community. In particular, forests often exhibit non-equilibrial dynamics with perturbations far from equilibrium (Frelich, 1991; Poulson and Platt, 1996; Woods, 2000), and this could violate the assumption of small perturbations in such models. This, combined with the considerable lag needed for juveniles to access the canopy following a gap-created pulse of light, may prevent a model of forest dynamics from to be approximated by the models of the general theory. It is also reasonable to believe the age structure could buffer variation in recruitment and prevent the relative non-linearity and the storage effect from operating.

The model simulates the survival and growth of populations of juvenile and adult trees in spatially homogeneous cells. Every individual within a cell experiences the same intensity of competition for light. Cells are independent from each other except through dispersal. Simulated this way, we discretize the spatial structure of forests into cells corresponding conceptually to a few individuals in a real forest. The spatially discrete nature of the model will allow us to determine if coexistence could occur in the presence of only temporal variation in light availability (through tests performed in a single cell). However, because cells are also connected by dispersal, we can also ask if the parameter space of the low light survival/high light growth trade-off allowing coexistence is affected by the spatial dimensions of disturbances.

In the model, competition for light is mechanistic. Light availability (in % of full sun) for juveniles in a cell follows an exponentially declining function of adult density: L(N) = 100*exp(-aN). The parameter a determines the carrying capacity of the cell, but it has no qualitative impact on the dynamics. The mortality rate of juveniles is a function of light availability: M(L)=m1exp(-Lm2). The parameter *m1* is the low light survival parameter (species specific) and *m2* shapes the decline of the relationship with light availability (m2 = 0.5 for every species). For the simulations with soil heterogeneity, *m1* is a linear function of soil fertility (S) : $m1(S)=m_0+bS$. Juvenile tree growth, in mm/yr of diameter growth, is also a function of light availability: G(L)=hL/((h/g)+L). The parameter h is the asymptotic high

light growth (species-specific) and g is the low light rate of increase in growth (g = 0.05 for every species). New seedlings are initialized with a stem diameter of 2 mm. Juveniles grow until they reach 10 cm in diameter and then become adults. Adults have a fixed size for simplicity. Adult mortality occurs in two ways: a baseline mortality rate (0.5%/yr) and disturbance mortality. The combined mortality rate is on average 1%/yr (which allowed us to obtain trees with life expectancies similar to those reported for tropical [Brokaw, 1985] and temperate [Runkle, 1981] forest trees). Disturbance mortality occurs at regular intervals and the mortality rate in a disturbance assumed to be the return interval (yr) X 0.5%. Dispersal among cells is spatially implicit. A fraction (D) of the seed rain comes from the pool of seeds produced by the whole community, while the remainder (1-D) is produced locally within a given cell. Except for low light survival (m1) and high light growth (h), all other parameters are equal for all species in the model.

We start by conducting simulations with two species to assess the general predictions of the model. For clarity, the shade tolerant species (high m1, low h) is species A and has fixed parameters. The intolerant species B has varying parameters. To assess stable coexistence, we ran two simulations for each set of parameters, one with either species A or B at 1% relative abundance among adults at the start of the run (there were no juveniles at the beginning of the simulation). According to Chesson's (2000a) criteria for coexistence, we concluded that coexistence was stable when both species could successfully invade when starting at low abundance (abundance assessed after 1000 yrs).

We first assessed the parameter space of the low light survival (m1)/high light growth (h) trade-off allowing coexistence as a function of the disturbance return interval (ranging from 1 yr to 100 yrs). For these simulations, only one cell was simulated to assure pure temporal variation in light availability. Second, we assessed how this parameter space was affected by soil spatial heterogeneity (i.e. a soil-related storage effect). In this scenario, light availability was spatially uniform, but soil fertility varied across the 10 cells. The average soil fertility was always 0, but we increased the range of S from 0 to 5 (with a uniform distribution). Soil fertility only affected survival of species B (b = 0.05). For this scenario and the following two, we compared extremely limited dispersal (D = 0.1) to uniform dispersal (D = 1). In the third scenario, we assessed how the parameter space was affected by

asynchronicity across space in the time of disturbance occurrence (but with a fixed return interval = 75 years) (the shifting successional hypothesis). In that scenario, disturbance is asynchronous across the 10 cells. Finally, we assessed how the parameter space is affected by creating variability in disturbance return interval across space (the "species sorting" hypothesis). In this scenario, the 10 cells have different and independent return intervals, ranging from 30 to 120 yrs (mean = 75 years).

Simulations with three species were also conducted in the same manner to assess multi-species coexistence for the scenarios with pure temporal heterogeneity, asynchronized disturbances and variability in disturbance return interval. The three species (A, B and C) were ranked by their high light growth and low light survival. High light growth was fixed, but low light survival varied for species B and C to find combination of parameters allowing coexistence. The disturbance return interval was 75 years. Time to fixation at three species was longer than in two species trials, so coexistence with the invisibility criterion was assessed after 2000 time steps. For each parameter combination, the initial abundance of the resident species is the result of a preliminary simulation of 5000 time steps with the two resident species.

6.6 Results

Simulation results are coherent with the predictions based on the general theory of coexistence in variable environments. First of all, the low-light survival/high light growth trade-off allows stable coexistence of two species through temporal variation in light availability alone (i.e., no spatial variation) (Fig 6.1A). The shape of the parameter space of the low light survival/high light growth trade-off allowing coexistence is thus not only a result of evolutionary/physiological constraints, it is also necessary for coexistence since a faster growing species must have a lower survival to coexist with a slow growing/high survival species (Fig 6.1A). The parameter space allowing coexistence is affected by the disturbance return interval (Fig 6.1B). The widest parameter space allowing coexistence is found at an intermediate disturbance return interval, which also corresponded to the highest variability in light availability (Appendix 6A1). At some disturbance return intervals, the dynamics was unstable, with the dominant species determined by initial relative abundance. This results from the interaction between a deterministic return interval and the time required

for saplings to reach the canopy, synchronizing the disturbance regime to the community dynamics. We did not observe such unstable dynamics when the return interval was modeled stochastically (results not shown). As predicted from Chesson's theory (2000a), the species difference in low light survival scales with variability in light availability (Fig 6.1C).

The Fig 6.2 confirms that coexistence based on temporal heterogeneity in light availability results from the relative non-linearity mechanism of coexistence. The recruitment of new individuals to the adult stage is relatively non-linear between species, the essential condition for this mechanism (Chesson, 2000b). Because the figure is on a log-log scale, the slope of the relationship is a measure of the relative non-linearity. The intercept is a measure of fitness inequality and the results correspond to the prediction that the most shade tolerant species is the strongest competitor. Because of the relative non-linearity and fluctuations in the intensity of competition, the species with the highest competitive ability at low resource (species A) can coexist stably with the species with the most non-linear response to competition (species B). As predicted by the general theory of coexistence in variable environments (Chesson, 1994, 2000b), only two species can coexist stably according to this mechanism (Table 6.1). Competitive exclusion is however extremely slow because of the long life expectancy of trees, leading to transient coexistence for extended periods of time (Appendix 6.2A). Over the long term, however, there is no partitioning along the trade-off axis and only the two most dissimilar species coexist at equilibrium.

The presence of spatial heterogeneity in the environment, either affecting shade tolerance (as here with soil fertility affecting m1) or the time of occurrence and return interval of disturbances, does favour coexistence (Fig 6.3, Table 6.2). Increasing soil heterogeneity can allow the coexistence of species that are increasingly dissimilar in their low light survival (Fig 6.3). The presence of strong dispersal limitation also affects coexistence. Soil heterogeneity and dispersal limitation increase spatial variation in relative abundance (Appendix 6.3A). These results are all evidence that the storage effect does act as a mechanism of coexistence. The simultaneous occurrence of sub-populations at different successional phases in the community (as a result of variation in the time of occurrence of disturbances) only has a weak effect on coexistence (Table 6.2). This source of spatial variability in light has a limited effect on the spatial distribution of the community (not

Figure 6.1 Lower and upper limits of the low light survival parameter (ml) and high light growth (h) of species B allowing coexistence with species A with only temporal variations in light availability. For all simulations, $ml_A = 0.5$ and $h_A = 1.0$. Panel A) The region between the lines of a given return interval represents any combination of high light growth and low light survival for species B allowing stable coexistence with species A. Panel B) The low light survival for species B allowing coexistence with A for a gradient of return interval (h is fixed at 1.6). Panel C) the standard deviation in light availability was recorded for every return interval once the dynamics has stabilized (monoculture of species A, $ml_A = 0.5$; $h_A = 1.0$; SD calculated from the 501-1000 yrs). The minimum low light survival of species B in panel B) for every disturbance return interval was plotted against the respective standard deviation in light availability. See text for details on the coexistence criteria.

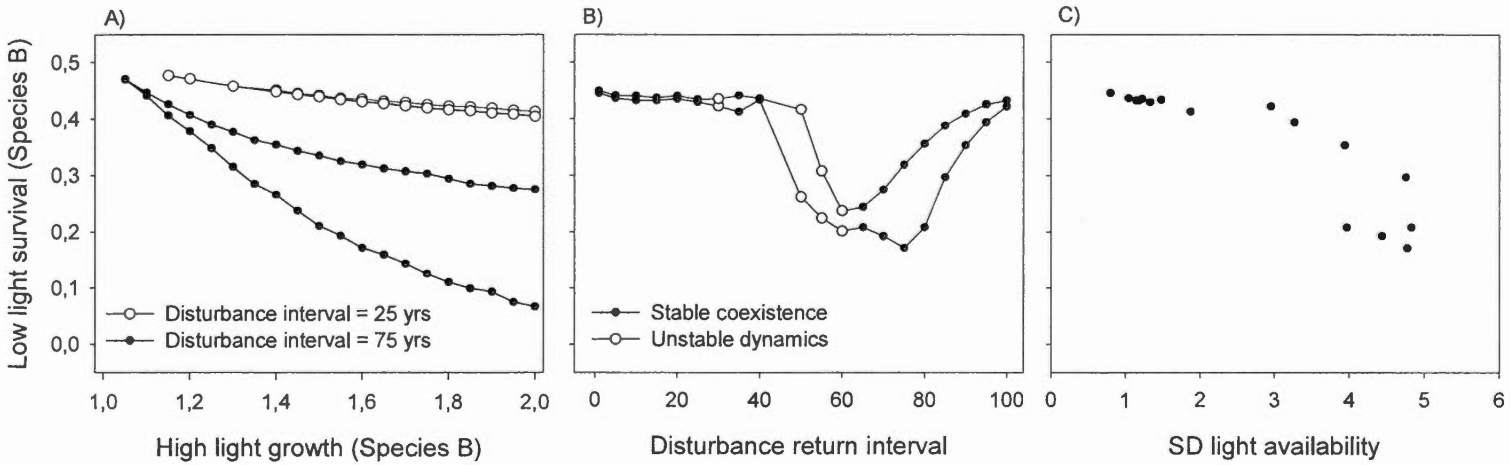


Figure 6.2 Relationship between recruitment per time step of species A and species B. Points represent recruitment in each of the last 250 yrs of a 1000 yrs simulation. The straight line represents a 1:1 relationship (perfect relative linearity). Disturbance return interval is 75; low light survival of species B is 0.2 and high light growth is 2.0. The simulation was initiated with equal abundances of each species.

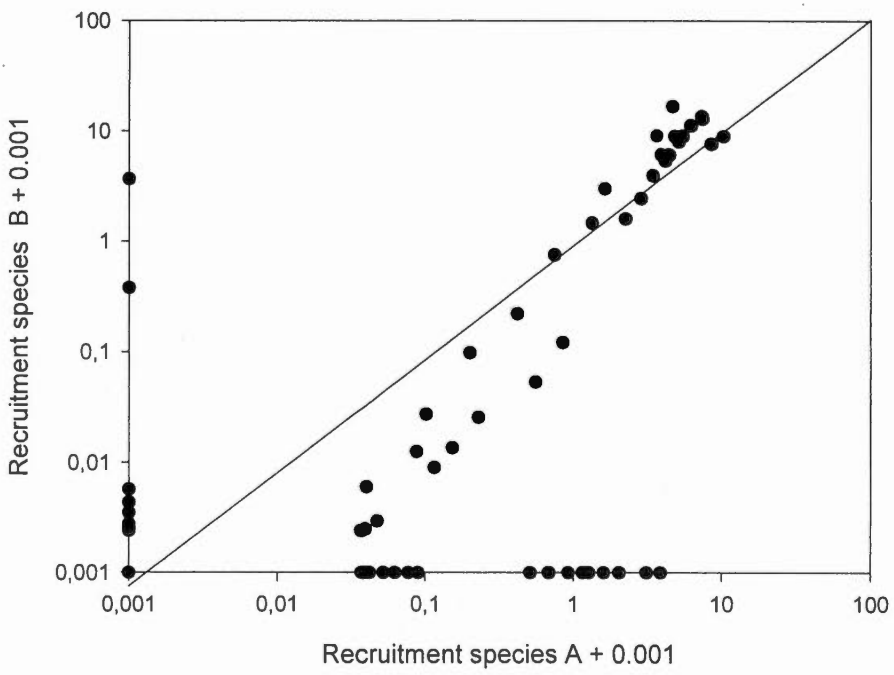


Table 6.1 Results of the tests for three species coexistence. The high light growth parameter was respectively set to 1.0, 1.6 and 2.0 for species A, B and C; the low light survival for species A was fixed at 0.5. Low light survival was varied from 0.5 to 2.0 for species B and C to find combination of parameters allowing coexistence. Disturbance return interval is 75 years. Dispersal limitations: D = 0.1. Three species coexistence ("YES") is obtained when all three species could invade a mixture of the other two species.

Source of heterogeneity	With dispersal limitations	No dispersal limitations
Temporal	N.A.	NO
Spatial – asynchronized disturbances	YES	NO
Spatial – heterogeneity in disturbance return interval	YES	NO
Spatial – random occurrence of disturbance events	NO	NO

Figure 6.3 Average low light survival of species B allowing coexistence as a function of soil heterogeneity (mean S = 0, range increases from 0 to 5). Only species B has a linear relationship between soil fertility and low light survival (see text for details).

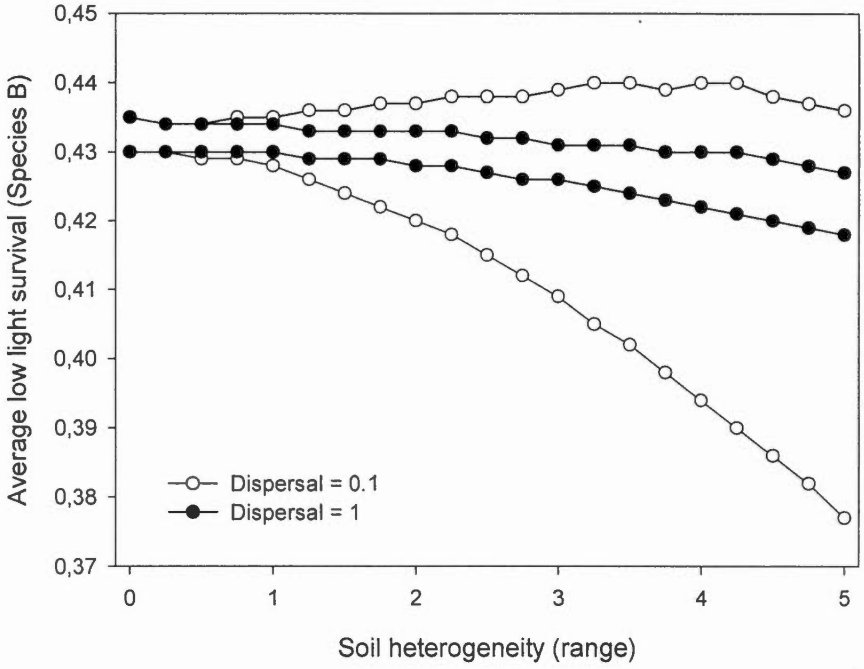


Table 6.2 Lower and upper limits of the low light survival parameter of species B (ml_B) allowing coexistence with species A (see parameters below) with spatial heterogeneity in disturbance. Simulations included 1) no spatial variation (only temporal variation in resource availability – for reference); 2) spatio-temporal variation resulting from asynchronicity in the occurrence of disturbance across the 10 simulated cells (but with a fixed return interval of 75 years), and 3) spatio-temporal variation resulting from spatial heterogeneity in the disturbance return interval (mean = 75 yrs, range is from 30 to 120). Default parameters: species A low light survival (ml_A) = 0.5 and high light growth (h_A) = 1.0, species B high light growth (h_B)= 1.6.

Source of heterogeneity		With dispersal limitations	No dispersal limitations
Only temporal	Lower limit	NA	0.171
	Upper limit		0.319
Spatially asynchronized disturbances	Lower limit	0.102	0.164
	Upper limit	0.290	0.317
Spatial variability in disturbance return interval	Lower limit	0	0
	Upper limit	0.376	0.414

shown), and thus a limited storage effect. The presence of spatial variability in the disturbance return interval has, however, a much more profound effect on the parameter space, especially when dispersal

limitation is important (Table 6.2). Both sources of spatial variability in light availability allow stable coexistence of more than two species over the long term (Table 6.1), but the parameter space allowing three species to coexist was extremely narrow, suggesting that no more than three species can coexist with this model configuration. Three species coexistence was not observed when disturbance events were simulated as random events (Table 6.1).

6.7 Discussion

The results from our simulations are in agreement with predictions from Chesson's (1994; 2000b) general theory of coexistence in variable environments. As predicted by the theory, the range of variation in low light survival between two species that can still allow coexistence increases with variation in competition and the environment. Variation in the intensity and return interval of disturbances, spatial asynchronicity in the occurrence of disturbances, spatial variability in disturbance frequency and soil properties are all sources of heterogeneity (in resource availability, or in the species' response to the resource) that contribute to coexistence. The agreement between the simulation results generated by our model and the predictions of Chesson's (1994, 2000b) general models suggests that the theory of coexistence in variable environments is robust to the presence of non-equilibrium dynamics. Indeed the non-equilibrium dynamics in our model that originated from feedback between population density and the limiting factor levels, combined with a strong time-lag between the increase of competition and recruitment in our model, generated considerable noise and even instability in the predictions of our model under certain conditions (Fig. 6.1A), but the essential predictions of Chessons's theory still held.

The simple simulation model of forest dynamics presented here is an alternative to much more complex simulation models such as SORTIE (Pacala et al., 1996), TROLL (Chave, 1999) and FORMIND (Köhler and Huth, 2007). In comparison to such models, our model relies on a fixed return interval of disturbances, and a simplification of the light environment. The return interval was kept fixed to facilitate the analysis of the simulation

results, but simulations with varying return intervals gave qualitatively similar results (not shown). The simplification of the light environment in our model, in comparison for instance to SORTIE, involved a simpler definition of the adult cohort structure (all adult trees were of the same size) and neglected shading by understorey individuals. A more complex treatment of the vertical structure of light within a cell would reduce the time lag between population growth and resource capture. Chesson's (1994, 2000a) model has no time lag, while ours has an extreme one, yet both models led to similar results.

Our model illustrates the specific processes and mechanisms that underly hypotheses relating shade tolerance differentiation, spatio-temporal fluctuations in light availability created by canopy gaps, and species coexistence. Perhaps the most common and intuitive prediction is that diversity should peak at an intermediate level of disturbance (Hubbell et al., 1999), the so-called intermediate disturbance hypothesis (IDH, Connell, 1978). It is now recognized that the IDH is a conceptual framework involving both relative non-linearity and the storage effect as coexistence mechanisms (Roxburgh et al., 2004, Shea et al., 2004). We found that the mechanism of relative non-linearity predicts that the parameter space allowing coexistence is largest at an intermediate level along the disturbance interval/severity axis.

However, the mechanism of relative non-linearity allows for stable coexistence of only two species. The formal mathematical argument to justify why the relative non-linearity allows only two species to coexist is given in Chesson (1994). Basically, this mechanism creates a maximum of two temporal niches: one for the species having the highest per capita growth rate under constant intensity of competition, the other for the species having the highest per capita growth rate under varying competition. In communities of three or more species, competition selects the two species that will maximise the relative non-linearity. This result is in sharp contrast with the widely held view that the low light survival/high light growth trade-off allows coexistence of multiple species (Pacala et al., 1996; Hubbell et al., 1999; Rees et al., 2001).

Perhaps, the contrast between with our results and other models of successional diversity, such as the IDH (Connell, 1978), might arise from the consideration of space. Models of successional diversity, such as the competition/colonization and the successional

niche models (Pacala and Rees, 1998), do not explicitly decompose the temporal and spatial mechanisms of coexistence. Such models usually either explicitly or implicitly assume some sort of a competition-colonization trade-off. Pioneer species differ from late successional species in many life-history traits, including their typically high fecundity, large dispersal and early age at reproduction (Tilman, 1990; Pacala et al., 1996; Rees et al., 2001). A correlation between disturbances and some competitive responses such as germination of seedbanks (Roxburgh et al., 2004) and fecundity (Kelly et Bowler, 2002) also shapes the response to competition and all of these traits contribute to a storage effect (Roxburgh et al., 2004).

In other models that do not include explicitly a competition-colonization trade-off,, a colonizing advantage is often implicitly assumed in the way initial recruitment is modelled following disturbances. Disturbances are commonly viewed as an extreme event that reset the community, eliminating all species from the site. Prior to disturbance, there should be a correlation between successional ranking and abundance, where late successional species would be expected to be more abundant. After a disturbance, if every species is recruited in equal proportion (the niche model of Pacala and Rees [1998]) or in proportion to the regional abundance (the shifting mosaic hypothesis, Watt [1947]), then disturbance will be most beneficial to pioneer species. The net effect is an implicit competition-colonization trade-off. In contrast to relative non-linearity, the competition-colonization trade-off allows an infinite number of coexisting species (Tilman, 1994).

Our model predicts that, even in the absence of a competition-colonization trade-off, spatial variation in disturbance synchronicity and return interval will generate a spatial storage effect that promotes coexistence. We simulated extreme cases where spatial heterogeneity of disturbances was maximal to facilitate the analysis. As predicted, the range of species dissimilarity in low light survival that allowed coexistence was positively related to the heterogeneity of disturbance occurrence (in synchronicity and return interval). Increasing dispersal limitations also reinforces the spatial storage effect by enhancing spatial variability in species distribution. The effect of variability in return interval was much more substantial than the effect of asynchronicity. In contrast to the situation with pure temporal fluctuations in light availability, both forms of spatial variability in disturbance allowed stable coexistence of three species. The parameter space was extremely narrow, however,

suggesting that coexistence would be unlikely with a more realistic simulation of the disturbance regime. For instance, by simply making the occurrence of a disturbance a random event that occurs on average every 75 years, thus creating spatio-temporal variation in disturbance intensity and synchronicity, we did not observe any coexistence. The incomplete destruction of the community by a disturbance could explain the weakness of the spatial storage effect to assure stable coexistence of more than two species. As mentioned above, the spatial storage effect relies on spatial variations in relative abundance. The accumulation of understorey juveniles tends to buffer temporal variations in light availability. Moreover, it slows the successional rate and thus, tends to prevent spatial heterogeneity in composition that should result from spatio-temporal variations in disturbance synchronicity and return interval.

It is worthwhile to mention in conclusion that forest ecologists should look at other traits associated with disturbances to find mechanisms of coexistence. The low light survival/high light growth is only one of the many possible strategies for trees to differentiate along a disturbance gradient (Loehle, 2000). The mechanisms illustrated here allow for stable coexistence, but they offer only a restricted space of traits in order to maintain elevated diversity. Our study focused on stable coexistence. Our simulation model was deterministic for the purpose of the analysis, but nature is not. A combination of a slow species turnover rates, demographic and environmental stochasticity, and elevated species similarity are all factors that could lead to extremely slow rates of competitive exclusion, with transient coexistence over an extremely long period of time (Hubbell, 2001; Scheffer and van Ness, 2006; Holt, 2006; Chapter 3). Perhaps, mechanisms favouring transient coexistence should also be considered for forest trees.

6.8 Appendix

Figure 6.1A Average and variability in light availability as a function of disturbance return interval. The moments of light availability were recorded for every return interval simulated at figure 6.1 (monoculture of species A, $m1_A = 0.5$; $h_A = 1.0$; statistics calculated from the 501-1000 yrs).

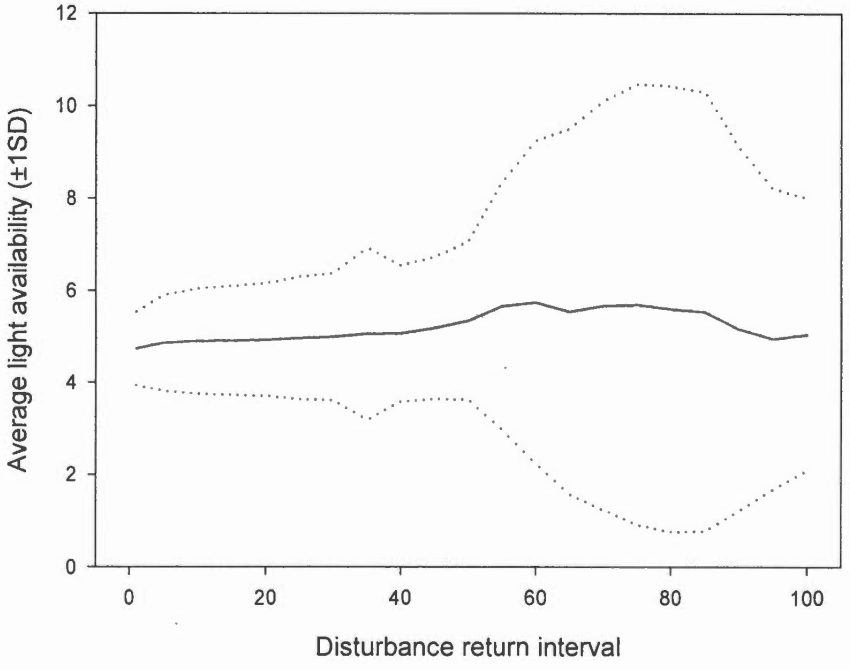


Figure 6.2A Species richness over time with only temporal variation in light availability. Disturbance return interval is 75 yrs. Survival trade-off with high light growth approximately as in figure 6.1A for the 75 years return interval: m1 = 1 – 1.8*exp(-1.3*h).

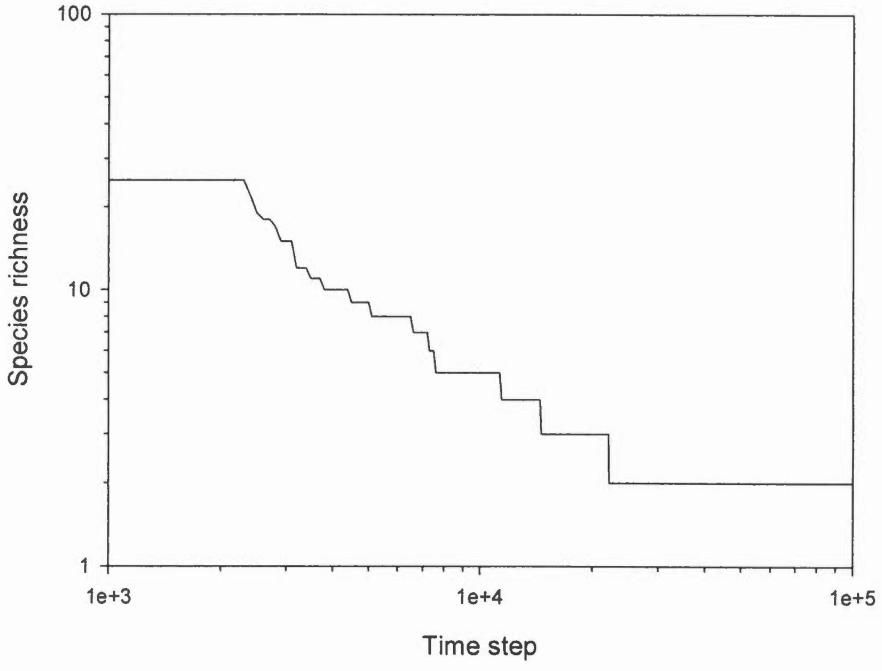
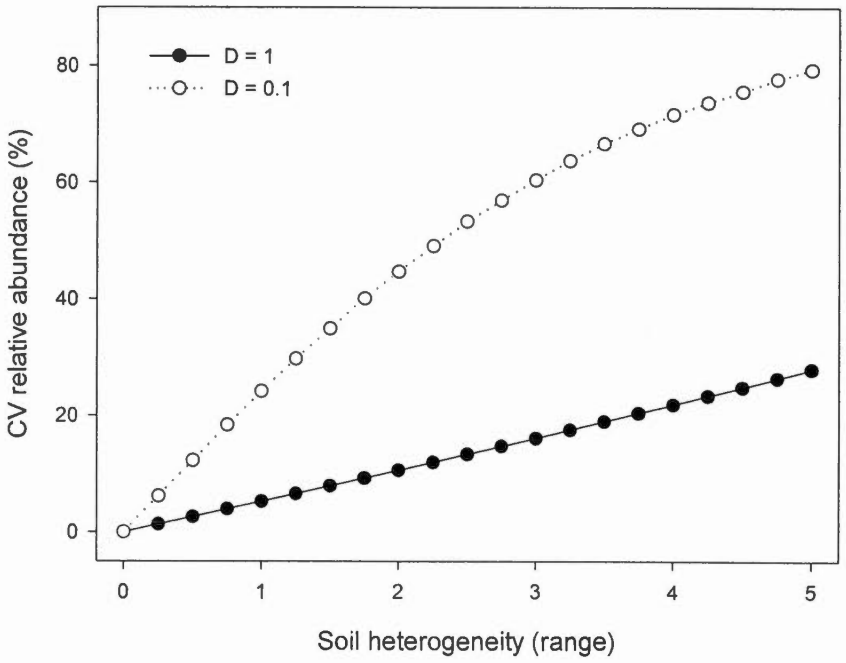


Figure 6.3A Spatial variability in relative abundance among adults (CV in %) as a function of soil heterogeneity (two species dynamics). 10 units are simulated. The parameters m1 and h are respectiely for species A and species B 0.5, 1.0, 0.42 and 1.6. Disturbance return interval is 25 yrs.



CONCLUSION GÉNÉRALE

C.1 Rappel des objectifs généraux

Deux objectifs généraux étaient poursuivis dans cette thèse. Tout d'abord, afin d'établir les bases pour la compréhension du récent changement de la dynamique de régénération de l'érable à sucre et du hêtre dans les forêts du sud du Québec, le premier objectif était de décrire la dynamique de ce phénomène et de tester des hypothèses sur son origine. Le second objectif, plus général, était de profiter de l'étude de ce phénomène pour approfondir la compréhension des mécanismes de la coexistence qui affectent la dynamique de ces espèces, et plus généralement, d'espèces forestières tolérantes à l'ombre.

Dans cette conclusion, nous commencerons par situer les résultats des études théoriques par rapport aux connaissances actuelles sur la théorie de la coexistence, puis nous nous servirons de ce cadre théorique pour interpréter les résultats empiriques.

C.2 Révision de la théorie sur la coexistence

Le premier résultat théorique d'importance est la démonstration d'un continuum entre les théories de la niche et neutre (Chapitre 3). Dans une communauté où il y a de la stochasticité démographique, la dérive aléatoire augmente avec la similarité entre les espèces, ainsi qu'avec l'immigration à partir de la méta-communauté. La combinaison de processus de sélection par la compétition et par le hasard résulte en un assemblage d'espèces complémentaires, dont la présence est stable dans le temps, ainsi que d'espèces redondantes dont la présence est toutefois transitoire. La structure spatiale des populations, la dispersion et les phénomènes aléatoires qui peuvent affecter les populations auront un impact supérieur à l'effet stabilisateur de la différentiation des niches lorsque la similarité entre les espèces est très élevée. De ce fait la capacité à prédire la distribution et l'abondance des espèces sera diminuée (Chapitre 4).

Lorsque la variabilité dans la réponse des espèces à leur environnement est élevée, la dynamique est encore plus difficile à prédire (Chapitre 5). La stochasticité démographique encouragera la dérive aléatoire et ralentira le taux de succession des espèces au sein d'une communauté. À l'inverse, la stochasticité environnementale (variabilité d'un moment à l'autre, corrélée entre individus au sein d'une espèce) dans le recrutement favorisera la stabilisation de la composition et la coexistence des espèces. La variabilité dans la réponse des espèces à leur environnement doit donc être considérée dans la comparaison de traits de vie entre espèces. À titre d'exemple, des différences statistiquement significatives entre des espèces sur la préférence de pH observées en serre ne seront pas nécessairement suffisantes pour assurer la coexistence de ces espèces dans un environnement où le sol est spatialement hétérogène.

Finalement, nous avons démontré que ce sont plusieurs mécanismes qui permettent la coexistence sur la base d'un compromis entre la survie à l'ombre et la croissance sous les trouées chez les arbres en sous-étage des forêts matures (Chapitre 6). La littérature assume généralement que les fluctuations temporelles de la lumière assurent l'hétérogénéité nécessaire à la coexistence d'espèces différentiées au long de cet axe de compromis. Le mécanisme de coexistence impliqué est la non-linéarité relative. Toutefois, si on ne considère que la variabilité temporelle de la lumière (et donc de l'intensité de la compétition pour cette ressource), ce mécanisme ne permet que la coexistence de deux espèces. La force de la coexistence augmente avec la variabilité de la disponibilité de la lumière, celle-ci étant maximale à un taux intermédiaire de formation des trouées. La coexistence de plusieurs espèces est rendue possible lorsque l'hétérogénéité environnementale permet l'effet de « storage », le second mécanisme de coexistence associé au compromis entre la survie et la croissance. L'effet de storage survient lorsque des variables environnementales créent de la variabilité spatiale dans le succès de régénération, par exemple la variabilité des propriétés du sol. La formation de trouées crée également un effet de storage par la création d'une mosaïque de stades successionnels et la variabilité dans la taille des trouées. Cet effet de storage est cependant très faible et les conditions permettant la coexistence à trois espèces sont très limitées.

Ces résultats théoriques bonifient le cadre théorique élaboré par Chesson (2000a) et discuté en introduction générale de la thèse. Chesson (2000a) considère seulement des modèles qui sont exempts de stochasticité démographique. Les simulations réalisées aux chapitres 3 et 5 démontrent bien que la dérive aléatoire existe même en présence de forts mécanismes stabilisateurs. En fait, nous avons démontré dans ces chapitres que la dérive aléatoire est une force qui s'oppose directement à la croissance des populations (taux de croissance à faible abondance dans le cadre de Chesson [2000a]). Moins la coexistence ou l'exclusion compétitive seront fortes, plus forte sera la dérive aléatoire, lente la succession et élevés les risques d'extinction aléatoire.

Nous avons aussi mis en valeur différents processus qui tendent à rapprocher les communautés du point neutre dans cet espace illustré en introduction, que ce soit par leur effet sur le terme d'inégalité ou sur le terme de stabilisation. L'ensemble de ces résultats permet de construire l'hypothèse du continuum. L'augmentation de la similarité entre les espèces affecte la force de la coexistence, diminuant le terme stabilisateur et augmentant la neutralité (Chapitre 3). Dans l'évaluation du terme de stabilisation, il est aussi très important de considérer la variabilité environnementale de l'axe qui différentie les espèces (Chapitre 6), tout comme la variabilité aléatoire de l'environnement (Chapitre 5). De même, la dispersion limitée est un mécanisme qui tend à réduire les inégalités entre les espèces et à rapprocher les communautés du point neutre (Chapitre 3). Et finalement, les processus qui augmentent la stochasticité démographique rapprochent la communauté du point neutre identifié à la figure I.1 par un effet à la fois sur le terme d'inégalité et sur le terme stabilisateur (Chapitre 5).

C.3 Coexistence de l'érable et du hêtre

Les chapitres 1 et 2 sont contrastés quant à leur support au modèle conceptuel présenté en introduction de la thèse. Au premier chapitre, nous avons tenté de modéliser la variabilité de la distribution spatiale de la régénération de l'érable à sucre et du hêtre à grandes feuilles en fonction de différentes variables environnementales ainsi qu'en fonction de la distribution spatiale des arbres parents. Les résultats vont généralement à l'encontre du modèle conceptuel. D'abord, nous avons trouvé une ségrégation spatiale de l'érable à sucre et du hêtre chez la très petite régénération, conformément au modèle, mais aussi une convergence des deux espèces, au niveau de leur distribution spatiale, chez les gaulis de forte taille. La

convergence des tiges de forte taille est associée aux endroits où la croissance était forte il y a une quinzaine d'années, suggérant que les deux espèces vont se recruter dans les endroits où surviennent des trouées. Les semis d'érable à sucre seraient davantage limités par la disponibilité de la lumière que ceux du hêtre, mais à terme les deux espèces vont accéder à la canopée dans les endroits où la lumière est abondante. Nous avons trouvé de nombreuses relations entre la distribution spatiale des espèces et les différentes variables environnementales étudiées; certaines sont cohérentes avec le modèle alors que d'autres ne le sont pas. Néanmoins, une analyse approfondie des résultats suggère que de nombreuses corrélations sont le fruit du hasard.

Au second chapitre, nous avons testé trois causes possibles au récent changement de la dynamique de régénération de l'érable et du hêtre. D'abord, nous avons testé si l'appauvrissement des sols par les précipitations acides a favorisé le hêtre au détriment de l'érable à sucre. Bien que nous ayons observé un déclin du recrutement de l'érable par rapport au hêtre, conformément à cette hypothèse, nous n'avons pas observé de déclin de croissance, ni même de relation entre l'abondance relative de ces espèces et les caractéristiques du sol. De même, l'épisode de dépérissement dans les années 1980 n'a pas stimulé le recrutement du hêtre, ni même contribué significativement à favoriser la croissance des tiges en sous-couvert. Par contre, nous avons observé un changement majeur au fil des quarante dernières années dans la proportion des tiges en forte croissance (libération). Il y a eu une diminution de la proportion de tiges en forte croissance dans la période de 1975-1990 et l'abondance de l'érable à sucre est négativement associée aux sites où cette dépression est la plus importante. La composition actuelle de la régénération dans les peuplements étudiés serait donc le résultat d'un changement dans le temps de la disponibilité de la lumière. L'ensemble de ces résultats est très cohérent avec le modèle de Poulson et Platt (1996), pour lequel l'abondance relative de l'érable et du hêtre dépend essentiellement de l'historique de petites perturbations de la canopée.

La variabilité démographique en forêt est très forte. De nombreux facteurs sont susceptibles d'affecter le succès de la régénération à accéder à la canopée : les défoliations par des insectes, les pathogènes, la sécheresse, la variabilité environnementale locale, la variabilité génétique... À titre d'exemple, Kobe (1996) et Bigelow et Canham (2002) ont

rapporté des relations entre la croissance et la lumière disponible pour ces espèces avec des coefficients de détermination (R^2) qui varient entre 0.17 et 0.79. Dans le chapitre 1, la qualité de l'évaluation des modèles diminue avec la classe de taille, ce qui serait cohérent avec la propagation de la stochasticité démographique avec le temps. Si on considère de surcroît que les deux espèces sont malgré tout très similaires, le cadre théorique illustré en introduction et bonifié plus haut prédit qu'une très forte hétérogénéité environnementale sera nécessaire pour assurer la coexistence.

Une explication possible aux résultats contrastés entre les chapitres 1 et 2 pourrait se trouver dans l'échelle spatiale à laquelle s'adresse le modèle conceptuel de coexistence. À la figure 3.1, on illustre comment l'inégalité entre deux espèces varie tout au long d'un gradient environnemental. Si l'étendue des conditions environnementales retrouvées dans une communauté se limite à un espace restreint aux environs du point neutre, il sera difficile de prédire la distribution et l'abondance des espèces. Le terme de stabilisation sera alors très faible parce que la superposition des niches est élevée. À l'inverse, si l'étendue de la variabilité environnementale couvre le gradient complet, alors le terme de stabilisation sera très fort.

Or, la variabilité environnementale tend à augmenter avec les échelles spatiale et temporelle considérées. L'autocorrélation spatiale des variables environnementales étant souvent forte (Lechowicz and Bell, 1991), il est plus probable que cette étendue soit large si on échantillonne des sites distants de plusieurs kilomètres que de quelques mètres. De même, elle sera plus large si on considère une fenêtre temporelle de 1000 ans qu'une fenêtre de 25 ans. Il est vraisemblable que la variabilité du sol et de la lumière rencontrée dans l'étude que nous avons réalisée à l'échelle locale ne soit pas suffisante pour assurer la coexistence stable de l'érable et du hêtre.

Sous cette perspective, le modèle conceptuel de la dynamique de l'érable à sucre et du hêtre ne serait pas un modèle de coexistence locale, mais plutôt de coexistence régionale. La coexistence locale serait transitoire (instable selon Chesson [2000a]) en raison du très faible taux de succession (faible différence entre espèces et durée de vie des générations). À cette échelle, l'historique de colonisation des sites, de perturbations extrêmes, de recolonisation et

la dispersion limitée de ces organismes seraient tous des facteurs qui favoriseraient cette coexistence transitoire.

C.4 Implications pour l'aménagement forestier

De nombreux résultats présentés dans cette étude sont d'intérêt pour l'aménagement forestier. Dans l'ordre dans lequel ils sont présentés dans la thèse, il est important de souligner que : 1) les caractéristiques de l'environnement ne permettent pas de prédire avec succès la distribution et l'abondance de la régénération dans l'espace d'une communauté locale ; 2) à l'échelle régionale, le succès de reproduction de l'érable à sucre par rapport au hêtre est affecté par l'historique de petites perturbations ; 3) par ailleurs, nous suspectons que la croissance des jeunes érables est actuellement très réduite par la compétition des gaules de hêtre ; 4) la dynamique d'espèces similaires est très lente et la stochasticité démographique diminue la prédictibilité de la réponse des espèces à l'environnement; et 5) l'augmentation de l'hétérogénéité de l'environnement, pour une disponibilité constante de la lumière, tend à favoriser la présence des espèces moins tolérantes à l'ombre.

Ces résultats suggèrent que la dynamique de l'érable à sucre et du hêtre à l'intérieur d'un peuplement est plutôt instable, sujette à de très fortes variations aléatoires. La rapidité à laquelle le système se rétablit après une perturbation de la composition ou de l'environnement est très lente et la trajectoire incertaine. La composition originale après une perturbation est susceptible d'avoir des effets plus importants sur l'abondance relative de ces espèces que les conditions environnementales post-perturbation. Pour les aménagistes forestiers intéressés à gérer ou modifier l'abondance relative de ces espèces, cette perspective a de profondes implications. Parce que les mécanismes de stabilisation sont plutôt faibles, l'ensemble de cette thèse suggère qu'une manipulation directe de l'abondance de ces espèces, par exemple par la plantation ou une élimination sélective des gaulis, aura un impact beaucoup plus considérable sur la composition future de la forêt qu'une manipulation de l'environnement par la récolte d'arbres ou la fertilisation.

APPENDICE : RÉPARTITION DES GAULES DE L'ÉRABLE À SUCRE ET DU HÊTRE À GRANDES FEUILLES DANS LE SUD DU QUÉBEC EN FONCTION DES PRINCIPALES VARIABLES CARTOGRAPHIQUES UTILISÉES POUR L'AMÉNAGEMENT FORESTIER

Dominique Gravel

A.1 Introduction

Cette thèse de doctorat a été amorcée à la suite de nombreuses observations véhiculées par des forestiers de terrain inquiets d'une possible recrudescence du hêtre à grandes feuilles parmi les gaules dans le sous-étage des érablières matures. Il existe dans la littérature des évidences de ce phénomène à de nombreux endroits dans l'aire de distribution de ces espèces (Ostrowsky and McCormack, 1986; Jenkins, 1997; Ray et al., 1999; Schwarcz et al., 2001; Forrester et al., 2003; Hane, 2003; Duchesne et al. 2005; Angers et al., 2005). À titre d'exemple, on a remarqué à la forêt de Hubbard Brook dans le New Hampshire que la densité des gaules de hêtre (< 10 cm au DHP) a augmenté de 5 fois de 1965 à 1997, alors que la densité des semis d'érable à sucre (< 50 cm de hauteur) a décliné de 20 fois et que la densité des petits gaulis (2-5 cm au DHP) a décliné de 80% (Hane, 2003). Ces observations sont confirmées également pour les Adirondacks (Jenkins, 1997). Des observations d'une abondance relative élevée du hêtre parmi les gaules ont été faites dans des forêts aménagées et anciennes (Brisson et al., 1994 ; Schwarcz et al., 2001; Angers et al., 2005). Néanmoins, la seule évidence concrète d'un changement dans le temps pour le sud du Québec est limitée à un échantillonnage sur 15 peuplements et sur une période de 10 ans (Duchesne et al., 2005).

L'objectif général de cette annexe est de dresser un portrait global de la situation pour l'ensemble des érablières du Québec. Il s'agit d'abord de confirmer ce phénomène pour les différentes régions où l'on retrouve ces espèces, ainsi que d'identifier les facteurs disponibles sur un support cartographique qui permettent de prédire l'abondance des gaules d'érable et de hêtre. Cette étude sera réalisée par l'analyse des Parcelles échantillons temporaires (PET) du Ministère des ressources naturelles et de la faune du Québec (MRNF) des campagnes d'inventaire des années 1970, 1980 et 1990. Ce travail permettra d'identifier les facteurs qui permettront aux aménagistes d'identifier les peuplements les plus susceptibles de présenter une abondance élevée des gaules de hêtre et qui devront faire l'objet d'une attention particulière.

A.2 Méthodologie

A.2.1 Source des données

Les données utilisées pour cette étude proviennent de l'inventaire de la ressource forestière fait par le MRNF. Les données sont regroupées sous trois programmes d'échantillonnage qui ont eu lieu dans les périodes de 1970 à 1977, 1980 à 1988 et 1992 à 2002. Ces périodes d'échantillonnage réfèrent aux programmes d'inventaires respectivement nommés premier, deuxième et troisième décennal. Les placettes utilisées sont des placettes temporaires, i.-e. aucune des placettes n'a été remesurée. Chaque programme d'inventaire offre donc une image instantanée du capital forestier du Québec pour une période donnée. Pour cette étude, je dispose des PET des domaines bioclimatiques 1 à 4, soit les domaines de l'érablière à caryer, l'érablière à tilleul, l'érablière à bouleau jaune et la sapinière à bouleau jaune. Les premier, deuxième et troisième programmes d'inventaire comprennent respectivement 30 986, 56 318 et 56 740 placettes. Ces données permettent de dresser un portrait très général de la situation pour l'ensemble du Québec.

La méthode d'échantillonnage est sensiblement la même pour les trois programmes d'inventaire. Il s'agit d'un inventaire aléatoire stratifié : l'emplacement des placettes est fixé aléatoirement, mais le nombre de placette d'inventaire pour chaque strate forestière est proportionnel au poids de la strate dans l'unité de sondage. Le programme d'inventaire commence par la cartographie des peuplements au moyen de la photo-interprétation. Les critères de stratification ont légèrement changé entre les programmes, avec un degré de raffinement croissant. Les critères de stratification cartographiques qui sont constants d'un programme à l'autre sont le groupement d'essence, la densité, la hauteur dominante et la présence d'une perturbation majeure et mineure. Les unités de sondage sont déterminées à partir des subdivisions naturelles (ex. bassin hydrographique) ou des territoires d'approvisionnement.

Les données d'inventaire des trois programmes d'échantillonnage proviennent de deux placettes d'échantillons de dimensions différentes. La plus grande placette sert au dénombrement des tiges de dimension marchande (> 9.1 cm au DHP) pour chaque espèce et par classe de diamètre et la plus petite placette sert au dénombrement des gaules (1.0 à 9.0 cm

au DHP) par espèce et classe de diamètre. Le premier programme a la particularité d'avoir été exécuté dans le système impérial et par conséquent les parcelles sont de 404.6856 m^2 pour les tiges marchandes (9.1444 cm et plus à 1.37 m de hauteur, mesurés par classe de 1 pouce) et de 40.4686 m^2 pour les gaulis (1.52 cm à moins de 9.144 cm à 1.37 m de hauteur, par classe de 1 pouce). Les second et troisième programmes sont quand à eux constitués d'une placette de 400 m^2, où les tiges de 9.1 cm et plus sont dénombrées par classe de 2 cm à 1.3 m de hauteur, et d'une parcelle de 40 m^2 pour les tiges de 1.1. cm à 9.0 cm à 1.3 m de hauteur, par classe de 2 cm. Par ailleurs, en forêt privée, de 1982 à 1985 on a appliqué des normes d'inventaire légèrement différentes, où les tiges étaient dénombrées dans des placettes de 500 m^2.

Une sélection des placettes a été nécessaire avant de procéder aux analyses. Pour ce faire, les espèces ont été regroupées en six catégories : ERS, HEG, feuillus tolérants et intermédiaires (FTO), feuillus intolérants (FIT), résineux (RES) et autres espèces (arbustives, AUT). Les placettes sont sélectionnées sur la base de la composition : l'érable à sucre et le hêtre à grandes feuilles sont au moins présents (1 tiges et plus) parmi les gaules ou les tiges marchandes et la surface terrière (incluant les gaules) des résineux représente moins de 25% de la surface terrière totale. La majorité des analyses porte sur les peuplements de classe d'âge de 70 ans et plus, incluant les classes jeune et vieille inequiennes (la classe d'âge est déterminée sur le terrain d'après la structure du peuplement).

A.2.2 Analyses statistiques

Le dispositif d'échantillonnage permet une comparaison par ANOVA de l'abondance des gaules d'érable à sucre et de hêtre à grandes feuilles entre les programmes d'inventaire. Pour cette analyse et les suivantes, les données ont été sous-échantillonnées aléatoirement pour assurer un dispositif factoriel balancé et ainsi pouvoir tester l'interaction facteur*espèce. La densité des gaules est aussi comparée entre les classes d'âge, les régions écologiques et les peuplements ayant subi une perturbation partielle (toutes perturbations confondues) pour le troisième décennal. Les densités de tiges ont été transformées par la racine carrée pour satisfaire aux conditions de normalité.

Une analyse de régression multiple de l'abondance relative des gaules d'érable à sucre par rapport au hêtre a également été réalisée pour modéliser la réponse à des variables

continues. Une procédure de sélection de variables pas à pas (procédure mixte) a été utilisée. La matrice des variables explicatives comprend les coordonnées géographiques, l'altitude, la surface terrière des tiges marchandes d'érable à sucre, de hêtre à grandes feuilles, de feuillus tolérants, de feuillus intolérants, de résineux et d'autres espèces, la pente, le drainage, le type de dépôt (till ou autre), l'épaisseur du dépôt (roc, très mince, mince et épais) et le pourcentage de pierrosité.

A.3 Résultats

L'abondance de l'érable à sucre et du hêtre à grandes feuilles parmi les tiges marchandes est demeurée sensiblement constante d'un programme d'inventaire à l'autre, à l'exception d'une légère diminution du hêtre à grandes feuilles au cours du troisième décennal (Figure A.1). La différence entre les décennaux est hautement significative (ratio de $F = 9.93$, $DL = 2$, $p < 0.0001$), hautement significative entre les espèces (ratio de $F = 728.51$, $DL = 1$, $p < 0.0001$) et l'interaction n'est pas significative (ratio de $F = 0.62$, $DL = 2$, $p = 0.538$). Notons cependant que le nombre élevé de parcelles (645/décennal) rend les petites différences hautement significatives. L'abondance parmi les gaules est cependant plus variable entre les décennaux. L'abondance de l'érable à sucre est demeurée constante d'une période à l'autre, mais le hêtre à grandes feuilles a augmenté considérablement. Le nombre de tiges à l'hectare de hêtre est passé de 429 pour le premier décennal à 914 pour le troisième décennal, soit une augmentation de 114%. La différence de densité des gaules entre les décennaux est hautement significative (ratio de $F = 18.79$, $DL = 2$, $p < 0.0001$), n'est pas significative entre les espèces (ratio de $F = 2.32$, $DL = 1$, $p = 0.1279$), mais l'interaction est hautement significative (ratio de $F = 25.65$, $DL = 2$, $p < 0.0001$). Cette analyse exprime donc des changements significatifs d'abondance absolue (effet décennal) et relative (interaction) en faveur du hêtre à grandes feuilles.

La densité des gaules diffère avec l'âge de façon hautement significative pour les deux espèces (Figure A.2, ratio de $F = 13.18$, $DL = 7$, $p < 0.0001$) pour le troisième décennal. La différence entre les espèces n'est pas significative (ratio de $F = 0.0221$, $DL = 1$, $p = 0.8819$), mais l'interaction est significative (ratio de $F = 2.05$, $DL = 7$, $p = 0.0466$), de sorte que le changement avec l'âge n'est pas le même pour les espèces. On retrouve une dominance de

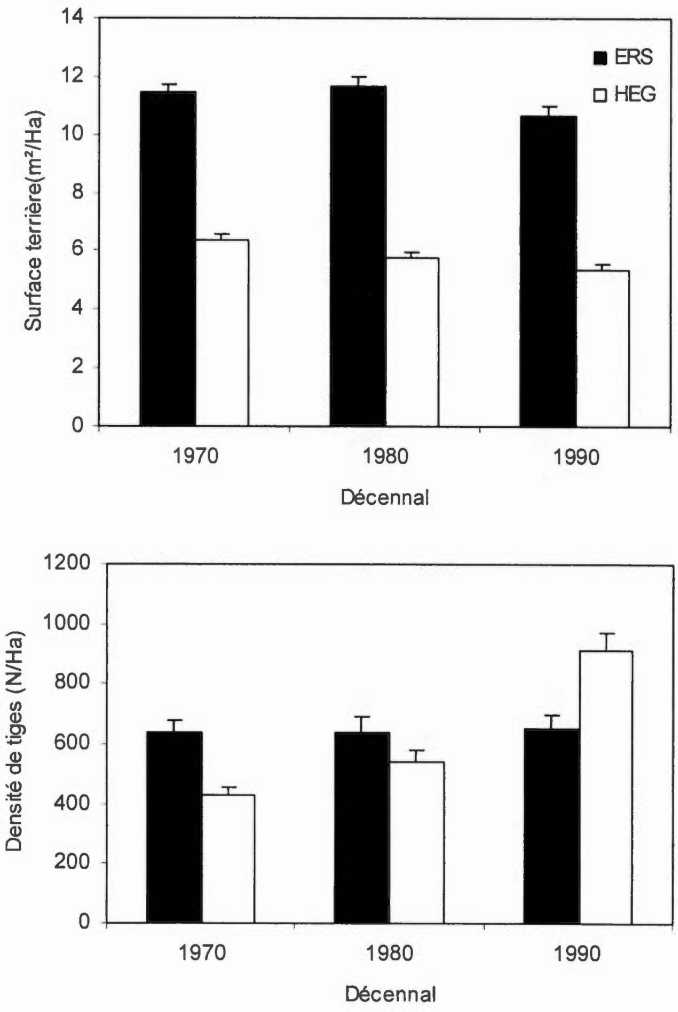
l'érable à sucre dans les jeunes peuplements, dominance qui s'estompe à partir de la classe de 50 ans (41-60 ans), et finalement une dominance du hêtre dans les classes d'âge plus élevées.

La surface terrière des tiges marchandes et la densité des gaules varient entre les régions écologiques. Pour la surface terrière, la différence entre les régions est significative (Figure A.3, ratio de $F = 2.1848$, $DL = 9$, $p = 0.00207$), la différence entre les espèces est hautement significative (ratio de $F = 288.5549$, $DL = 1$, $p < 0.0001$), tout comme l'est l'interaction région*espèce (ratio de $F = 2.8302$, $DL = 9$, $p = 0.0026$). La différence de densité des gaules entre les régions n'est pas significative (Figure A.3, ratio de $F = 1.76$, $DL = 9$, $p = 0.0713$), mais la différence entre les espèces est hautement significative (ratio de $F = 27.94$, $DL = 1$, $p < 0.0001$), tout comme l'est l'interaction région*espèce (ratio de $F = 6.21$, $DL = 9$, $p < 0.0001$). Il n'y a pas de patron de variation entre les régions cohérent pour la surface terrière. La densité des gaules est plus variable pour l'érable à sucre que pour le hêtre. À l'exception des régions correspondant au domaine de l'érablière à Caryer (1a) et au Bas-St-Laurent (4f) où l'abondance du hêtre est plus faible, l'abondance de cette espèce est plus ou moins constante d'une région à l'autre. À l'inverse, l'érable à sucre a une densité variable qui culmine dans les régions écologiques du domaine de l'érablière à bouleau jaune. L'écart entre les deux espèces est maximal pour les régions correspondant au domaine de l'érablière à tilleul (2a-2b et 2c) et au contrefort des Laurentides au nord de la ville de Québec (Chalevoix, Saguenay et Portneuf, région 4d).

La présence d'une perturbation partielle augmente significativement la densité des gaules (Figure A.4, ratio de $F = 23.59$, $DL = 1$, $p < 0.0001$). Conformément aux résultats précédents, les deux espèces ont une densité différente (ratio de $F = 56.55$, $DL = 1$, $p < 0.0001$), mais la magnitude de la réponse à la présence de perturbation est la même pour les deux espèces (interaction perturbation*espèce, ratio de $F = 3.07$, $DL = 1$, $p = 0.0801$).

L'abondance relative des gaules de l'érable à sucre par rapport au hêtre pour le programme du troisième décennal n'est pas bien expliquée par les différentes variables continues analysées (Table A.2). Bien que les différentes variables sélectionnées soient toutes

Figure A.1 Comparaison de la surface terrière des tiges marchandes (haut) et de la densité de gaules (bas) entre les inventaires des décennaux 1970, 1980 et 1990. Les peuplements analysés sont de classes d'âge > 70 ans, incluant les structures inéquiennes. Les parcelles échantillons temporaires ont été sous-échantillonnées aléatoirement pour avoir un dispositif factoriel balancé (645 parcelles par programme d'inventaire). Les barres d'erreur



égalent l'erreur type.

Figure A.2 Comparaison de la densité des gaules entre les différentes classes d'âge de l'étage supérieur pour le troisième décennal. Les parcelles échantillons temporaires ont été sous-échantillonnées aléatoirement pour avoir un dispositif factoriel balancé (46 parcelles par classe d'âge).

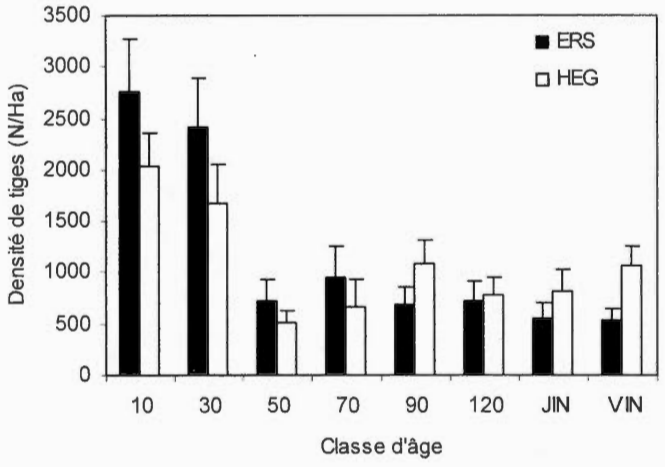


Figure A.3 Comparaison de la surface terrière des tiges marchandes (haut) et de la densité de gaules (bas) par région écologique (les codes sont définis au Tableau A.1) pour le troisième décennal. Les parcelles échantillons temporaires ont été sous-échantillonnées aléatoirement pour avoir un dispositif factoriel balancé (78 parcelles par région écologique).

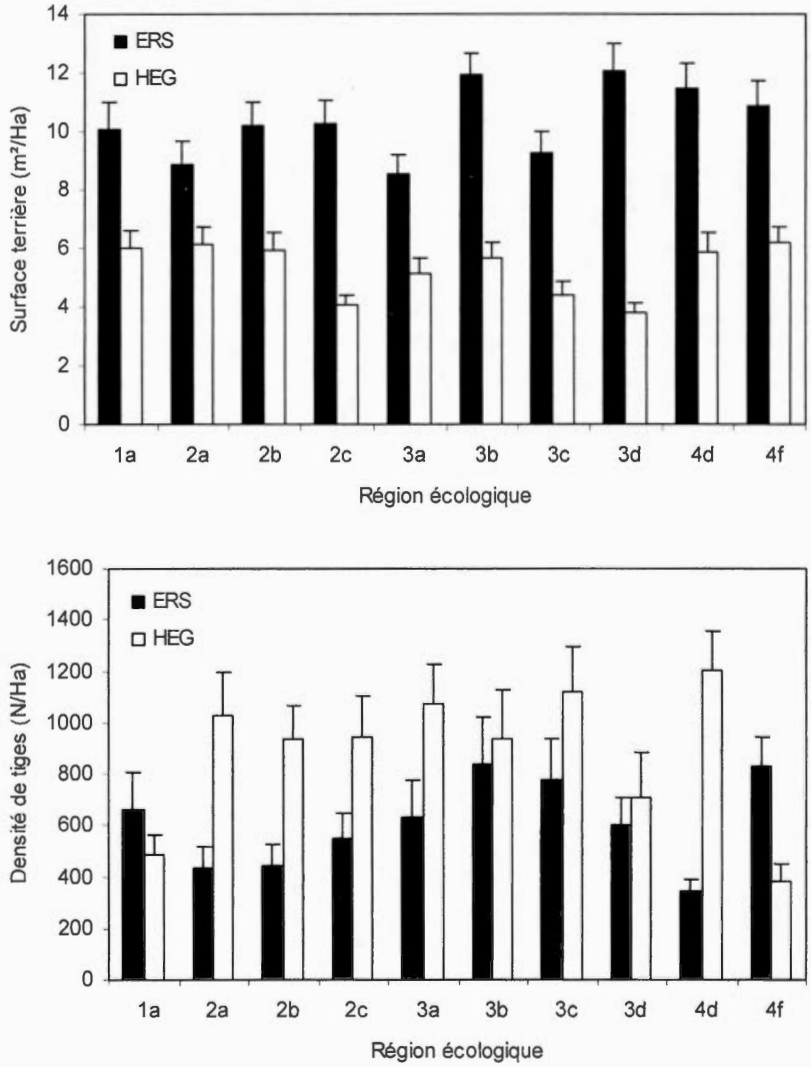


Table A.1 Définition des codes de région écologique

Code	Domaine bioclimatique	Sous-domaine	Région écologique
1a	Érablière à caryer	-	Plaine du bas Outaouais et de l'archipel de Montréal
2a	Érablière à tilleul	Ouest	Collines de la basse Gatineau
2b	Érablière à tilleul	Est	Plaine du St-Laurent
2c	Érablière à tilleul	Est	Coteaux de l'Estrie
3a	Érablière à bouleau jaune	Ouest	Collines de l'Outaouais et du Témiscamingue
3b	Érablière à bouleau jaune	Ouest	Collines du lac Nominingue
3c	Érablière à bouleau jaune	Est	Hautes collines du bas Saint-Maurice
3d	Érablière à bouleau jaune	Est	Coteaux des basses Appalaches
4d	Sapinière à bouleau jaune	Est	Hautes collines de Charlevoix et du Saguenay
4f	Sapinière à bouleau jaune	Est	Collines des moyennes Appalaches

Figure A.4 Comparaison de la densité des gaules pour des peuplements non perturbés et des peuplements qui ont subi une perturbation partielle (tous types confondus, date inconnue) pour le troisième décennal. Les parcelles échantillons temporaires ont été sous-échantillonnées aléatoirement pour avoir un dispositif factoriel balancé (545 parcelles par niveau de perturbation).

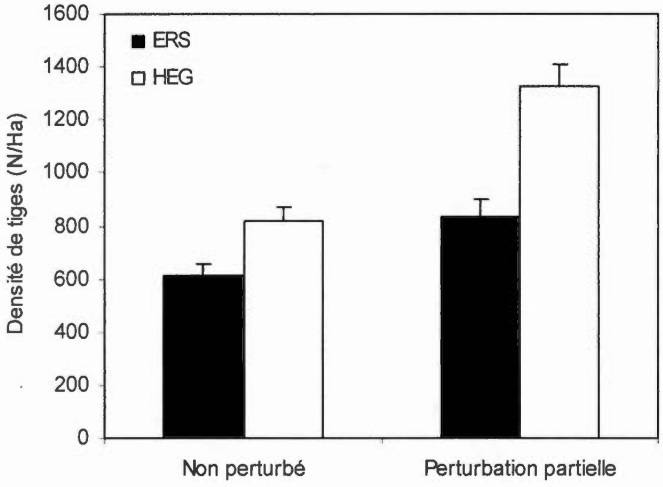


Table A.2 Résultats de la régression multiple de l'abondance relative de l'érable à sucre pour le troisième décennal après sélection des variables pas à pas (procédure mixte, seuil de p = 0.05). Les variables rejetées de l'analyse sont l'altitude, la surface terrière des feuillus intolérants et des résineux, le type de dépôt (till versus autres), l'épaisseur du dépôt, le drainage et le pourcentage de pierrosité. Seulement les peuplements des classes de 70 ans plus sont analysés. N = 2195., $R^2 = 0.099$, $R^2_{ajusté} = 0.096$.

Source	Estimé	DL	Somme des carrés	Ratio de t	Prob > t
Ordonnée origine	0.2741	0.8297		0.33	0.741
Latitude	0.0479	0.0148	1.5335	3.25	0.001
Longitude	0.0268	0.0036	8.0949	7.46	<.001
ST ERS	-0.0042	0.0013	1.5678	-3.28	0.001
ST HEG	-0.0185	0.0018	14.5765	-10.01	<.001
ST FTO	0.0035	0.0018	0.5495	1.94	0.052
ST AUT	0.0166	0.0053	1.4145	3.12	0.002
Pente	0.0017	0.0008	0.7703	2.30	0.022

significatives au seuil de p = 0.05, moins de 10% de la variance de l'abondance relative de l'érable à sucre parmi les gaulis est expliquée par l'ensemble des variables. La composition de la canopée ne permet pas de prédire de façon satisfaisante la composition de la régénération, ni même les facteurs de site tels l'altitude, le type de dépôt, la pente et le drainage. Des régressions polynomiales ont été tentées sur les variables individuellement pour vérifier si les relations peuvent être non linéaires, sans plus de succès.

A.4 Discussion

Les résultats présentés ici ne permettent pas de tester formellement des hypothèses quant aux causes de l'abondance élevée du hêtre à grandes feuilles dans certains peuplements. Ces résultats permettent néanmoins de soulever certaines hypothèses qui enrichissent la réflexion entreprise dans cette thèse. Cette analyse permet de dresser un portrait très général de la situation actuelle que l'on retrouve au Québec. Sans nul doute, le résultat le plus frappant est le changement de la composition de la strate gaulis. Alors que l'abondance de l'érable à sucre demeure inchangée d'un programme d'inventaire à l'autre, celle du hêtre augmente considérablement. Il s'agit d'un changement d'une double nature. L'augmentation de la densité absolue implique soit une dynamique du hêtre qui n'est pas à l'équilibre, ou bien un changement de la capacité de support (plus de ressources). L'augmentation de l'abondance relative implique également un changement de la hiérarchie compétitive entre les deux espèces.

Les résultats présentés dans cette étude montrent qu'à l'exception de la classe d'âge, il n'est pas possible de prédire à partir des variables cartographiques couramment utilisées dans quels peuplements se trouveront les densités les plus élevées de hêtre à grandes feuilles. Les peuplements les plus jeunes ont une abondance relative de l'érable à sucre beaucoup plus élevée et cette différence s'amenuise avec le vieillissement des peuplements. Ce résultat est cohérent avec les nombreux modèles de coexistence chez ces espèces qui placent l'érable vainqueur en début de succession (Forcier, 1975; Canham, 1988; Poulson et Platt, 1996). Par contre, les perturbations partielles ne font qu'augmenter la densité des gaules, sans affecter l'abondance relative. Comme ces perturbations ne donnent pas d'avantage initial à l'érable à sucre, à l'issu de la fermeture du couvert et de la compétition pour la lumière, il se pourrait que le hêtre soit avantagé par ces perturbations. Les perturbations auront augmenté la densité

de tiges en sous-étage pour une certaine période, et la sélection par la mortalité se fera plus rapidement chez l'érable que le hêtre.

Il y a cependant des différences considérables entre les régions et un patron intéressant ressort de cette analyse. Les régions les plus sensibles ne sont pas celles situées à la marge de la distribution du hêtre, ni systématiquement celles qui sont situées sur les sites pauvres du bouclier canadien, mais plutôt les peuplements du domaine de l'érablière à tilleul, ainsi que des peuplements associés au contrefort des Laurentides sur la rive-nord de la région de Québec. Ces résultats ne concordent pas avec les prédictions de changements d'abondance sous l'effet des changements climatiques. Non plus d'ailleurs avec les sols les plus fortement appauvris par les précipitations acides (Ouimet, 2004). Les régions où la différence d'abondance est la plus élevée correspondent davantage aux régions du Québec les plus densément peuplées, pour certaines où l'agriculture y est bien établie, ou d'autres pour lesquelles la récolte forestière y est très intensive depuis longtemps. Ce résultat n'apporte pas en soit de réponse à la cause du phénomène, mais il nous oriente néanmoins vers un rôle possible de l'historique de perturbation de ces forêts.

Il est légitime de se demander si la structure actuelle des gaules prédit un changement de la composition future des érablières. Est-ce que l'on peut prédire la composition future de la canopée à partir de la composition de la régénération? Et plus particulièrement, quelle devrait être l'abondance relative de l'érable par rapport au hêtre pour maintenir la composition actuelle de la canopée?

La mortalité des tiges en sous-couvert est à l'origine de la structure en J inversée des peuplements inéquiens. La transition d'une classe de diamètre à la suivante est une fonction de sa capacité à survivre et à croître en sous-étage. La déviation d'une population à sa structure théorique permet de prédire si elle est en augmentation ou en diminution (Condit et al., 1998). Si par exemple l'abondance des gaules dans un peuplement est supérieure à l'abondance théorique, sous environnement constant, ces tiges migreront vers les classes supérieures et il y aura augmentation de la densité dans les classes supérieures. Dans une dynamique à deux espèces, pour maintenir une population équivalente dans les classes supérieures de DHP, l'espèce ayant le taux de mortalité le plus élevé nécessitera davantage de

tiges en régénération (Condit et al., 1998). Par analogie, l'érable à sucre, qui a une survie en sous-couvert inférieure à celle du hêtre (Kobe *et al.*, 1995; Poulson et Platt, 1996; Beaudet *et al.*, 1999; Caspersen et Kobe, 2001), devra donc avoir une abondance relative supérieure parmi les gaules pour maintenir une abondance égale dans la canopée. D'autant plus que la composition de la canopée est actuellement largement dominée par l'érable à sucre.

Au terme de ce raisonnement, il est raisonnable de conclure que si les conditions environnementales se maintiennent dans le temps, la composition des forêts feuillues du sud québécois devrait changer en faveur du hêtre dans les décennies à venir.

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